T31257

91-406046
5 v. (xxvii, 1183 l.) : ill. ; 28 cm

Bibl. v.4, 775-972

THE UNIVERSITY OF CHICAGO

PRJSMON

QL999.L11

1. Insects--Feeding and feeds.
2. Insects--Anatomy.
3. Mouth--Anatomy.

I. Title. pw

DATE 18 July 1990

LABANDEIRA, CONRAD CHRISTOPHER — 11-9-50
Author — Birth Date

USE OF A PHENETIC ANALYSIS OF RECENT HEXAPOD MOUTHPARTS FOR THE DISTRIBUTION OF HEXAPOD FOOD RESOURCE GUILDS IN THE FOSSIL RECORD
Title of Dissertation

Geophysical Sciences — Ph. D. — Summer 1990
Department or School — Degree — Convocation

Permission is herewith granted to the University of Chicago to make copies of the above title, at its discretion, upon the request of individuals or institutions and at their expense.

Signature of writer

Extensive Quotation or Further Reproduction of This Material by Persons or Agencies Other than the University of Chicago May Not Be Made without the Express Permission of the Writer.

8-30-90 — 1,216
Date filmed — Number of pages

NOTE:

THE UNIVERSITY OF CHICAGO

USE OF A PHENETIC ANALYSIS OF RECENT HEXAPOD MOUTHPARTS FOR THE DISTRIBUTION OF HEXAPOD FOOD RESOURCE GUILDS IN THE FOSSIL RECORD

VOLUME ONE

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE PHYSICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
DEPARTMENT OF GEOPHYSICAL SCIENCES

BY
CONRAD CHRISTOPHER LABANDEIRA

CHICAGO, ILLINOIS
AUGUST, 1990

ACKNOWLEDGEMENTS

For a dissertation of this type to be produced, five essential requirements must be realized: (i) an intrinsic desire to do the research and write the dissertation, (ii) financial support, (iii) a conducive academic atmosphere of colleagues, (iv) technical support, mostly in the form of a good library and a computation center, and (v) personal support from loved ones. Below, I acknowledge the importance that each of these five necessities have provided toward the completion of this dissertation.

The two major financial sources for this dissertation were a teaching assistantship from the University of Chicago and three summers d two winters of construction work at Dritex, Inc., of Palatine, Illinois. Thanks go to the University of Chicago and to Jim Powell of Dritex; Jim took a gamble on employing an impecunious graduate student as a journeyman drywall taper and finisher in the Northwest Suburbs. Without both of these sources this project cold never have been attempted. Ancillary financial assistance in the form of grant support came from the American Geological Institute, Geological Society of America, Obering Fund of the Department of Geophysical Sciences, Paleontological Society and Sigma Xi (the National Scientific Research Society). Many thanks go to these professional organizations.

From the more distant past, I thank Robert Bereskin, formerly of California State University-Fresno, who first academically introduced me

to the joys of paleobiology. My interest in paleobiology was encouraged at the Masters level by Peter Sheehan of the Milwaukee Public Museum, who made laboratory facilities available to a California farm kid new to the meterological and dietary realities of the Midwest. Peter was a supportive mentor and an esteemed colleague in my pursuit of a thesis on trilobites.

During the more recent past I have had informative and thought-provoking discussions regarding the initial stages of this project from Frank M. Carpenter of Harvard University, Jarmila Kukalová-Peck of Carleton University in Ottawa, John Kethley of the Field Museum of Natural History, and Michael C. LaBarbara and Thomas J.M. Schopf of the University of Chicago. Special thanks goes to James Ashe of the University of Kansas-Lawrence who provided me inspiration, intellectual guidance and encouragement during the middle and late stages of this project. I especially thank David M. Raup of the University of Chicago, who apparently has the patience of Job and the exceptional quality of offering understanding and encouragement when a graduate student most needs it. Jack Sepkoski of the University of Chicago graciously provided attention to the details of the cluster analysis and FORTRAN programs that I was using. Tom Baumiller, Mike Foote and Mark Patzkowsky provided assistance in the intricacies of FORTRAN programming. Finally I thank the members of my dissertation committee--James Ashe, David Jablonski, David Raup, Jack Sepkoski and Leigh Van Valen--who provided critical evaluation of the final report.

My foray into the vast and diverse entomological and paleoentomological literature was assisted by several outstanding members of the library staff at the Crerar Library at the University of Chicago, including William Garrity, Christa Modschiedler, Ammiel Prochovnick, Brenda Rice, Harriet Schnoor, Patricia Swanson, James Vaughn and Kathleen Zar. They obtained for me a seemingly endless stream of interlibrary loans from periodicals such as *Biologica Gabonica*, *Odonatologica* and *Papua New Guinea Agricultural Journal*. I will never forget a whimsical comment by William Garrity regarding one of his (and mine) time-honored gems of entomologica "esoterica:" a 1933 article in *Victorian Naturalist* entitled "Notes on Silverfish." All these sources of data, however, were essential to the dissertation.

Dorothy Ragan and Joyce Weil of the Computation Center provided valuable guidance and the necessary changes in the default settings of the mainframe computer software to allow the processing of my unusually large data matrix. Without their help I could not have run the cluster analysis program. The University of Chicago Division of the Physical Sciences supplied Computation Center funds for the cluster analysis program.

The undertaking and completion of this dissertation relied not only on the experience, attention to scholarship and technical expertise of the afore-mentioned colleagues, but also the moral and emotional support that only loved-ones can provide. In this context I convey my gratitude to my parents, Mathew and Margaret Labandeira, of Riverdale, California, who allowed my imagination to run wild as an adolescent. They probably now realize that my turning over logs for crawly things and poking sticks in the mudpuddles in "the back of the slough" was not only playing hookey from farm responsibilities while they were gone, but also the start of an avocation. I express my sincere and deepest thanks to June Labandeira, my wife, confidant and source of inspiration, who has supported me in every way, particularly during times of dissertation disillusionment. Although my stepdaughters Aliza and Naomi Fulton have heard more than they care about insects, fossils and rocks, their intellectual development is a source of inspiration. It is to all the loved-ones in my life that I dedicate this dissertation.

CONTENTS

VOLUME ONE

Page

ACKNOWLEDGEMENTS ii

LIST OF TABLES xiii

LIST OF FIGURES xiv

ABSTRACT xxiv

Chapter

1. INTRODUCTION 1
2. JUSTIFICATION AND GOALS OF THIS STUDY 5
3. PREVIOUS RESEARCH 19
    - 3.1. A Brief Overview of Mouthpart Morphology Research 19
    - 3.2. Studies Focusing on the Functional Morphology of Hexapod Mouthparts 24
4. INSECT MOUTHPART STRUCTURE AND RELATED ISSUES 27
    - 4.1. Insect Head Segmentation 27
    - 4.2. The Problem of Homology 30
    - 4.3. General Insect Mouthpart Structure 32
    - 4.4. A General Account of Mouthpart Structure 33
        - 4.4.1. Labrum and Epipharynx 35
        - 4.4.2. Mandibles 36
        - 4.4.3. Hypopharynx 37
        - 4.4.4. Maxillae 38
        - 4.4.5. Labium 39
    - 4.5. Departures from the Generalized Mouthpart Condition 40
5. THE VARIABLES: USE OF HEAD AND MOUTHPART FEATURES AS FUNCTIONAL INDICATORS 44
    - 5.1. Rationalization for Choice of Characters 44

5.2. **Functional Significance of the Characters Used** 49
5.3. **Character-Group I: Head Shape and General Mouthpart-Related Characters** 50
5.3.1. Head Shape (Character 1) 51
5.3.2. Rostrum or Proboscis Development (Character 2). 53
5.3.3. Genal Region or Malar Space (Character 3). 55
5.3.4. Gular or Hypostomal Region (Character 4). 55
5.3.5. Lorum, or Mandibular Plate (Character 5). 59
5.3.6. Frontal and Vertical Region (Character 6). 59
5.3.7. Head Protractability and Retractability (Character 7) 60
5.3.8. Head-Associated Feeding Modifications (Character 8). 60
5.4. **Character-Group II: Sense Organs of the Head** 62
5.4.1. Antennae (Character 9) 62
5.4.2. Ocelli, Pseudocelli and Stemmata (Character 10). 64
5.4.3. Compound Eyes (Character 11) 65
5.5. **Character-Group III: General Features of Mouthpart Apparati** 67
5.5.1. Mouthpart Placement on the Head Capsule (Character 12). 67
5.5.2. Mouthpart Basic Type (Character 13) 70
5.5.3. Stylet Number (Character 14) 72
5.5.4. Mouthpart Symmetry (Character 15) 72
5.5.5. Food Pump (Character 16) 74
5.5.6. Protractability/Retractability of Major Food Reaching Mouthpart Elements (Character 17) 76
5.6. **Character-Group IV: The Clypeal Region** 77
5.6.1. Shape of the Entire Clypeal Complex (Character 18) 77
5.6.2. Clypeal Subsegmentation (Character 19). 78
5.7. **Character-Group V: The Labral Region**. 80
5.7.1. Shape of the Labral Main-Body (Character 20) 81
5.7.2. Labral Subsegmentation (Character 21). 81

5.7.3. Modification of the Distal Margin (Character 22). 82
5.7.4. Labral Participation in Multielement Mouthpart Structure (Character 23) 84
5.8. **Character-Group VI: The "Pharyngeal" Region**. 85
5.8.1. Cibarium Size (Character 24) 85
5.8.2. Hypopharynx Type (Character 25) 86
5.8.3. Epipharynx Type (Character 26) 90
5.9. **Character-Group VII: The Mandibular Region**. 93
5.9.1. Mandibular Articulation (Character 27) 94
5.9.2. Mandibular Type (Character 28) 95
5.9.3. Mandibular Dentition (Character 29) 100
5.9.4. Musculation and Mandibular Motion (Character 30). 107
5.9.5. Mandibular Participation in Multielement Mouthpart Structure (Character 31) 107
5.10. **Character-Group VIII: The Maxillary Region** 109
5.10.1. General Condition of the Stipes (Character 32). 111
5.10.2. Maxillary Main-Body Segmentation (Character 33) 112
5.10.3. Maxillary Appendages (Character 34) 113
5.10.4. Maxillary Palpus Segmentation (Character 35). 115
5.10.5. Maxillary Palpus Type (Character 36) 118
5.10.6. Maxillary Palpus Aspect-Ratio (Character 37) 121
5.10.7. Galeal Modifications (Character 38) 124
5.10.8. Lacinial Modifications (Character 39) 130
5.10.9. Maxillary Participation in a Multielement Mouthpart Structure (Character 40) 137

5.11. Character-Group IX: The Labial Region 139
  5.11.1. General Shape of Labial Main-Body (Character 41) 142
  5.11.2. Labial Main-Body Segmentation (Character 42). 144
  5.11.3. Labial Appendages (Character 43) 145
  5.11.4. Labial Palpus Segmentation (Character 44). 148
  5.11.5. Labial Palpus Type (Character 45) 151
  5.11.6. Glossae Modifications (Character 46) .157
  5.11.7. Paraglossae Modifications (Character 47) 162
  5.11.8. Labial Palpus Aspect-Ratio (Character 48) 166
  5.11.9. Labial Participation in a Multielement Mouthpart Structure (Character 49) 168
5.12. Summary Statement. 173

6. THE SAMPLES: A REPRESENTATIVE SELECTION OF INSECT DIVERSITY. .177
6.1. Organization and Coverage of Data 177
6.2. Criteria for Selecting Data. 181
  6.2.1. Data Source Quality. 181
  6.2.2. Citation to the Genus or Species Level 182
  6.2.3. Multiple Data Sources. 182
  6.2.4. Primary and Secondary Data Sources. 182
6.3. Summary Statement. 183

7. CLUSTERING METHODOLOGY 184
7.1. Appropriateness of Cluster Analysis 184
7.2. Similarity Index 185
7.3. Clustering Algorithm 187
7.4. Interpretation of the Dendrogram 188

8. RESULTS AND INTERPRETATION 195
8.1. A Brief History of Studies of Mouthpart "Classes" 195
  8.1.1. Aristotle. 196
  8.1.2. The Impact of Fabricius. 197
  8.1.3. Metcalf and Recent Contributions. 199

8.1.4. The Confounding of Structural, Functional and Taxonomic Terms. 205
8.2. **Nomenclature and Documentation of the Derived Groups** 209
8.3. **Mandibulate Series** 212
8.3.1. General Features of the Mandibulate Series 212
8.3.2. Entognathate Class (Class 1). .216
8.3.3 Monocondylate Class (Class 2). .223
8.3.4. Adult-Ectognathate Class (Class 3). .232

VOLUME TWO

8.3.5. Larval-Ectognathate Class (Class 4). .264
8.3.6. Maxillolabiate Class (Class 5). .291
8.3.7. Raptorial-Ectognathate Class (Class 6). 306
8.3.8. Mortar-and-Pestle Class (Class 7). .316
8.3.9. Rostrate Class (Class 8). .325
8.3.10. Rhynchophorate Class (Class 9). .335
8.3.11. Pectinate Class (Class 10) .345
8.3.12. Mouthbrush Class (Class 11) .356
8.3.13. Mandibulobrustiate Class (Class 12) .374
8.3.14. Sericterate Class (Class 13) .387
8.4. **Mandibulo-Canaliculate Series**. 414
8.4.1. General Features of the Mandibulo-Canaliculate Series 414
8.4.2. Fossate-Complex Class (Class 14) .417
8.4.3. Tubulomandibulate Class (Class 15) .428
8.4.4. Mouthhook Class (Class 16) .439

8.5. **Labellate Series** 454
  8.5.1. General Features of the Labellate Series 454
  8.5.2. Haustoriate Class (Class 17) .457
  8.5.3. Labellate Class (Class 18) .469
8.6. **Siphonate Series** 489
  8.6.1. General Features of the Siphonate Series 489
  8.6.2. Siphonate Class (Class 19) .492
  8.6.3. Siphonomandibulate Class (Class 20) .510
8.7. **Glossate Series**. 519
  8.7.1. General Features of the Glossate Series. 519
  8.7.2. Glossate Class (Class 21) .519

VOLUME THREE

8.8. **Stylate-Nonhaustellate Series**. 537
  8.8.1. General Features of the Stylate-Nonhaustellate Series. 537
  8.8.2. Entognathous-Stylate Class (Class 22) .541
  8.8.3. Ectognathous-Stylate Class (Class 23) .550
8.9. **Stylate-Haustellate Series** 563
  8.9.1. General Features of the Stylate-Haustellate Series 563
  8.9.2. Segmented-Beak Class (Class 24) .571
  8.9.3. Buccal-Cone Class (Class 25) .594
  8.9.4. Mouthcone Class (Class 26) .605
  8.9.5. Monostylate/Distylate Class (Class 27) 621
  8.9.6. Distylate/Tetrastylate Class (Class 28) 634
  8.9.7. Hexastylate Class (Class 29) .644
  8.9.8. Tristylate Class (Class 30) .667
  8.9.9. Tubulostylate Class (Class 31) .679
  8.9.10. Siphonostylate Class (Class 32) .690

8.10. Agnathate Series 700
8.10.1. General Features of the Nontrophic Series. 700
8.10.2. Reduced-Trophic Class (Class 33) 704
8.10.3. Nontrophic Class (Class 34) .728
8.11. Summary Statement. 739

9. LIMITATIONS OF THE DATA AND RESULTS. 761
9.1. Reliability of Mouthpart Morphology Data Sources. 761
9.2. Reliability of Variable Characterizations 762
9.3. Taxonomic and Morphologic Representation 763

10. SUMMARY AND CONCLUSIONS. 765
10.1. Basic Patterns of the Results. 765
10.2 The Role of Metamorphosis in Mouthpart Diversity 768
10.3 The Phenomenon of Convergence. 770
10.4. Mouthpart Aptation and the Success of Insects 771
10.5 Future Research. 773

VOLUME FOUR

REFERENCES CITED 775

VOLUME FIVE

Appendix Page

A. CHARACTER-STATES FOR INSECT MOUTHPART PART AND HEAD CHARACTERIZATION .974

B. REFERENCE LIST OF INSECT TAXA DESCRIBED BY MOUTHPART MORPHOLOGY AND DIETARY DATA 987

C. DATA ENTRIES OF MOUTHPART MORPHOLOGY CHARACTER-STATES FOR RECENT INSECT SPECIES 1078

D. EXTANT HEXAPOD DIVERSITY 1107

E. REGISTER AND DETAILS OF FOSSIL INSECT LOCALITIES REFERRED TO IN THIS STUDY 1116

F. DOCUMENTATION OF FOSSIL INSECT OCCURRENCES FOR MOUTHPART CLASS GEOCHRONOLOGY 1126

LIST OF TABLES

Table Page

1. Scheme of text nomenclature of ordinal, supraordinal and metamorphic designations 2
2. Model for Application of Recent Mouthpart Classes to the Fossil Record 17
3. Summary of gross characteristics of hexapod mouthparts. 34
4. Percentage representation of families, species and subadult forms for each order in the data-set 179
5. A morphologically-based classification of Recent hexapod mouthparts. 191
6. A brief, selected history of insect mouthpart classification. 200
7. Standardized names used for projecting, food-reaching organs described in this study. 208
8. Data-set taxa whose mouthpart series assignments are unusual for their respective order 745

LIST OF FIGURES

Figure Page

1. Matrix showing relationships between character-groups, characters, and type of characters for cases of the data-set 47
2. Character-states of Character 1: Head shape 52
3. Character-states of Character 2: Rostrum or proboscis 54
4. Character-states of Character 3: Genal region or malar space. 56
5. Character-states of Character 4: Gula or hypostome. 58
6. Character-states of Character 7: Head protractability/retractability. 61
7. Character-states of Character 9: Antennae 63
8. Character-states of Character 11: Compound eyes. 66
9. Character-states of Character 12: Mouthpart placement on head capsule. 68
10. Character-states of Character 13: Mouthpart basic type .71
11. Character-states of Character 14: Mouthpart stylet number. 73
12. Character-states of Character 15: Mouthpart symmetry 75
13. Character-states of Character 18: Shape of the clypeal complex 79

Figure Page

14. Character-states of Character 22: Modification of distal labral margin 83

15. Character-states of Character 25: Hypopharynx type 87

16. Character-states of Character 26: Epipharynx type. 91

17. Character-states of Character 28: Mandibular type. 97

18. Character-states of Character 29: Mandibular dentition 102

19. Character-states of Character 35: Maxillary palpus segmentation. 116

20. Character-states of Character 36: Maxillary palpus type. 120

21. Character-states of Character 37: Maxillary palpus aspect ratio. 122

22. Character-states of Character 38: Galeal modifications 125

23. Character-states of Character 39: Lacinial modifications 131

24. Character-states of Character 45: Labial palpus type 152

25. Character-states of Character 46: Glossal modifications. 158

26. Character-states of Character 47: Paraglossal modifications. 163

27. Proportional representation of the most abundant hexapod orders in the data-set 180

28. Summary of cluster analysis dendrogram of Recent hexapod mouthparts. 190

29. Overview of the Entognathate Mouthpart Class 218

Figure Page

30. Cluster analysis dendrogram of taxa comprising the Entognathate Mouthpart Class 220

31. Geochronologic history of the Entognathate Mouthpart Class 222

32. Overview of the Monocondylate Mouthpart Class 226

33. Cluster analysis dendrogram of taxa comprising the Monocondylate Mouthpart Class 228

34. Geochronologic history of the Monocondylate Mouthpart Class. 230

35. Overview of the Adult-Ectognathate Mouthpart Class. 237

36. Cluster analysis dendrogram of taxa comprising the Adult-Ectognathate Mouthpart Class. 241

37. Geochronologic history of the Adult-Ectognathate Mouthpart Class 254

38. Overview of the Larval-Ectognathate Mouthpart Class. 268

39. Cluster analysis dendrogram of taxa comprising the Larval-Ectognathate Mouthpart Class. 272

40. Geochronologic history of the Larval-Ectognathate Mouthpart Class. 279

41. Overview of the Maxillolabiate Mouthpart Class. 294

42. Cluster analysis dendrogram of taxa comprising the Maxillolabiate Mouthpart Class 300

43. Geochronologic history of the Maxillolabiate Mouthpart Class 302

44. Overview of the Raptorial-Ectognathate Mouthpart Class 309

Figure Page

45. Cluster analysis dendrogram of taxa comprising the Raptorial-Ectognathate Mouthpart Class 311

46. Geochronologic history of the Raptorial-Ectognathate Mouthpart Class 313

47. Overview of the Mortar-and-Pestle Mouthpart Class. 318

48. Cluster analysis dendrogram of taxa comprising the Mortar-and-Pestle Mouthpart Class. 320

49. Geochronologic history of the Mortar-and-Pestle Mouthpart Class. 323

50. Overview of the Rostrate Mouthpart Class. 327

51. Cluster analysis dendrogram of taxa comprising the Rostrate Mouthpart Class. 329

52. Geochronologic history of the Rostrate Mouthpart Class 331

53. Overview of the Rhynchophorate Mouthpart Class. 338

54. Cluster analysis dendrogram of taxa comprising the Rhynchophorate Mouthpart Class 340

55. Geochronologic history of the Rhynchophorate Mouthpart Class 342

56. Overview of the Pectinate Mouthpart Class. 347

57. Cluster analysis dendrogram of taxa comprising the Pectinate Mouthpart Class. 349

58. Geochronologic history of the Pectinate Mouthpart Class. 351

59. Overview of the Mouthbrush Mouthpart Class. 359

Figure Page

60. Cluster analysis dendrogram of taxa comprising the Mouthbrush Mouthpart Class. 362

61. Geochronologic history of the Mouthbrush Mouthpart Class 364

62. Overview of the Mandibulobrustiate Mouthpart Class. 377

63. Cluster analysis dendrogram of taxa comprising the Mandibulobrustiate Mouthpart Class. 379

64. Geochronologic history of the Mandibulobrustiate Mouthpart Class 381

65. Overview of the Sericterate Mouthpart Class 391

66. Cluster analysis dendrogram of taxa comprising the Sericterate Mouthpart Class. 396

67. Geochronologic history of the Sericterate Mouthpart Class. 401

68. Overview of the Fossate-Complex Mouthpart Class. 419

69. Cluster analysis dendrogram of taxa comprising the Fossate-Complex Mouthpart Class. 421

70. Geochronologic history of the Fossate-Complex Mouthpart Class. 423

71. Overview of the Tubulomandibulate Mouthpart Class. 430

72. Cluster analysis dendrogram of taxa comprising the Tubulomandibulate Mouthpart Class. 433

73. Geochronologic history of the Tubulomandibulate Mouthpart Class. 435

74. Overview of the Mouthhook Mouthpart Class 443

Figure | Page

75. Cluster analysis dendrogram of taxa comprising the Mouthhook Mouthpart Class. 446

76. Geochronologic history of the Mouthhook Mouthpart Class. 448

77. Overview of the Haustoriate Mouthpart Class 460

78. Cluster analysis dendrogram of taxa comprising the Haustoriate Mouthpart Class. 462

79. Geochronologic history of the Haustoriate Mouthpart Class. 464

80. Overview of the Labellate Mouthpart Class. 471

81. Cluster analysis dendrogram of taxa comprising the Labellate Mouthpart Class. 476

82. Geochronologic history of the Labellate Mouthpart Class. 481

83. Overview of the Siphonate Mouthpart Class. 495

84. Cluster analysis dendrogram of taxa comprising the Siphonate Mouthpart Class. 499

85. Geochronologic history of the Siphonate Mouthpart Class. 504

86. Overview of the Siphonomandibulate Mouthpart Class. 512

87. Cluster analysis dendrogram of taxa comprising the Siphonomandibulate Mouthpart Class. 515

88. Geochronologic history of the Siphonomandibulate Mouthpart Class 517

89. Overview of the Glossate Mouthpart Class. 522

Figure | Page
90. Cluster analysis dendrogram of taxa comprising the Glossate Mouthpart Class. 527
91. Geochronologic history of the Glossate Mouthpart Class 529
92. Overview of the Entognathous-Stylate Mouthpart Class. 544
93. Cluster analysis dendrogram of taxa comprising the Entognathous-Stylate Mouthpart Class. 546
94. Geochronologic history of the Entognathous-Stylate Mouthpart Class 548
95. Overview of the Ectognathous-Stylate Mouthpart Class. 554
96. Cluster analysis dendrogram of taxa comprising the Ectognathous-Stylate Mouthpart Class. 557
97. Geochronologic history of the Ectognathous-Stylate Mouthpart Class 559
98. Overview of the Segmented-Beak Mouthpart Class 575
99. Cluster analysis dendrogram of taxa comprising the Segmented-Beak Mouthpart Class 580
100. Geochronologic history of the Segmented-Beak Mouthpart Class 585
101. Overview of the Buccal-Cone Mouthpart Class 598
102. Cluster analysis dendrogram of taxa comprising the Buccal-Cone Mouthpart Class 600
103. Geochronologic history of the Buccal-Cone Mouthpart Class. 602
104. Overview of the Mouthcone Mouthpart Class. 609

Figure Page

105. Cluster analysis dendrogram of taxa comprising the Mouthcone Mouthpart Class 614

106. Geochronologic history of the Mouthcone Mouthpart Class 616

107. Overview of the Monostylate/Distylate Mouthpart Class 624

108. Cluster analysis dendrogram of taxa comprising the Monostylate/Distylate Mouthpart Class 627

109. Geochronologic history of the Monostylate/Distylate Mouthpart Class 629

110. Overview of the Distylate/Tetrastylate Mouthpart Class 636

111. Cluster analysis dendrogram of taxa comprising the Distylate/Tetrastylate Mouthpart Class 639

112. Geochronologic history of the Distylate/Tetrastylate Mouthpart Class 641

113. Overview of the Hexastylate Mouthpart Class 647

114. Cluster analysis dendrogram of taxa comprising the Hexastylate Mouthpart Class 655

115. Geochronologic history of the Hexastylate Mouthpart Class 657

116. Overview of the Tristylate Mouthpart Class 669

117. Cluster analysis dendrogram of taxa comprising the Tristylate Mouthpart Class 672

118. Geochronologic history of the Tristylate Mouthpart Class 674

Figure | Page

119. Overview of the Tubulostylate Mouthpart Class 682

120. Cluster analysis dendrogram of taxa comprising the Tubulostylate Mouthpart Class 685

121. Geochronologic history of the Tubulostylate Mouthpart Class 687

122. Overview of the Siphonostylate Mouthpart Class 692

123. Cluster analysis dendrogram of taxa comprising the Siphonostylate Mouthpart Class 696

124. Geochronologic history of the Siphonostylate Mouthpart Class 698

125. Overview of the Reduced-Trophic Mouthpart Class 708

126. Cluster analysis dendrogram of taxa comprising the Reduced-Trophic Mouthpart Class 713

127. Geochronologic history of the Reduced-Trophic Mouthpart Class 716

128. Overview of the Nontrophic Mouthpart Class 731

129. Cluster analysis dendrogram of taxa comprising the Nontrophic Mouthpart Class 733

130. Geochronologic history of the Nontrophic Mouthpart Class 736

131. Percentage distribution of mouthpart classes in the Recent hexapod fauna 743

132. Geochronologic distribution of mouthpart classes of the Mandibulate Series 751

Figure Page

133. Geochronologic distribution of mouthpart classes of the Mandibulo-canaliculate, Labellate, Siphonate, Glossate, and Stylate-Nonhaustellate Mouthpart Series 753

134. Geochronologic distribution of mouthpart classes of the Stylate-Haustellate and Nontrophic Series. 754

135. A comparison of familial diversity versus mouthpart class diversity for hexapods during the Phanerozoic. 758

ABSTRACT

An examination using 49 head- and mouthpart variables on 1365 recent hexapod OTU's at the species or genus level was performed to assess the structural discreteness of hexapod mouthparts. Adult and immature stages of all 34 extant hexapod orders and over 70% of the 997 families were characterized from approximately 1200 primary and secondary sources from the entomological literature. This examination was performed by using a BMDP2M cluster analysis program of unordered, multistate, qualitative to semiqualitative variables, using a Jaccard similarity index and a centroid clustering algorithm. Each cluster of OTU's exhibiting similar mouthpart form was then assessed for the dietary spectrum of its constituent taxa. The following results were obtained:

1. The mouthparts and associated head structures of modern hexapods (Insecta and their sister-group, Parainsecta) are structurally divisible into 34 fundamental groups (mouthpart classes).
2. In terms of mouthpart classes, taxonomic diversity of the modern insect fauna is dominated (58%) by three mandibulate, solid food consuming, mouthpart classes: adult-ectognathates, larval-ectognathates and sericterates. The next four in rank order are mouthpart classes of diverse fluid-feeders (labellate, siphonate, segmented-beak and mouthhook) that cumulatively account for 75% of all hexapod diversity.

3. For most mouthpart classes there is moderate to high levels of structural convergence among phyletically unrelated taxa.

The association between mouthpart class and diet is moderate to strong and allows for diet to be a predictable outcome of mouthpart structure. Since mouthpart classes are associated with characteristic diets to some extent, and many insect clades have respectable fossil records, each mouthpart class was tracked through the geologic record. The following patterns were obtained.

1. The geochronologic record of hexapod mouthpart innovation and diversity during the Later Paleozoic to the Cenozoic was characterized by a five-phase process. By the Early Devonian three specia lized and generalized mouthpart classes were present and there is indication of a fourth, adult-ectognathate. During the Late Carboniferous several mandibulate mouthpart classes existed, representing a respectable variety of head form for the sequestering of solid and fluid plant and animal food. The first filtering mouthpart classes appeared during this time. This second expansion was succeeded by a third phase of several mouthpart classes associated with the initial radiation of holometabolous insects during the Permian. Virtually all of these mouthpart classes were involved in the consumption of fluid foods from plant and arthropods. This proliferation of holometabolous mouthparts reached its climax during the fourth phase of the Late Triassic and Early Jurassic, in which four additional mouthpart classes of stylate dipterans and siphonapterans invaded fluid-feeding niches, including plant secretions, insect honeydew and vertebrate blood. Lastly there was a modest addition of two

(possibly three) mouthpart classes associated with but not necessarily originating contemporaneously with angiosperms.

2. There is strong indication that the proliferation of mouthpart structure (as indicated by mouthpart classes) is decoupled from the secular trend of insect taxonomic diversification. Whereas family-level data indicates a gradual, semiexponential rise in hexapod taxa with a steep upswing during the Cretaceous and Tertiary, 91% of mouthpart classes appear by the Middle Jurassic and subsequently asymptote significantly prior to the burst of taxonomic diversification. Inclusion of mouthpart data from from Paleozoic insects (not studied) corroborates this conclusion.
3. Based on (2) above there is a strong suggestion that glossate and siphonate mouthparts antedate angiosperms, with whom they are currently intimately coevolved. This diachroneity forces re-evaluation of the traditional view of the early, obligate relationship between angiosperm and pollinator diversity, indicating that at least some insect clades coevolutionarily associated with angiosperms evolved by lateral transfer from a preangiospermous flora and not *in situ* coevolution.
4. The pattern of hexapod mouthpart diversity through time supports the ecological saturation hypothesis, wherein the number of ecological roles is fixed relatively early during the evolution of an ecosystem, rather than the expanding resources hypothesis, characterized by the gradual addition of ecological roles to the ecosystem during evolutionary time. Accordingly, whereas the Recent hexapod fauna is taxonomically diverse and highly differentiated in terms of

mouthpart classes and diet, the Early Mesozoic insect fauna was significantly less diverse taxonomically but shared almost the same level of mouthpart structure, indicating a similar dietary spectrum.

CHAPTER 1

INTRODUCTION

> No set of organs in the body of an insect vary in form to a greater degree than do the mouthparts (Comstock 1940, p.42).

> No other anatomical character tells so much about an animal's habits as its mouth parts (MacNamara 1924, p. 94).

These two statements succinctly pose a common theme that has long been associated with hexapod[1] morphology--namely that hexapod mouthparts are extraordinarily diverse (Frost 1959) and that they can potentially reveal much about a hexapod's life-habits. In conjunction with Popham's claim that "feeding is the most fundamental of animal activities" (1962, p.436), then not only does a large chunk of potentially analyzable structure exist at the cephalad end of hexapods but also this structure can be used to elucidate the dynamic association between mouthpart type and diet of insects. Given the voluminous literature on descriptions of mouthpart form and structure (see Snodgrass 1928, Matsuda 1965, Denis

---

[1] I am using the term Hexapoda to refer to that clade, usually designated as a class, that includes (i) all apterygote groups and (ii) the derived group, Pterygota, although the term Insecta has been used to encompass both groups as well (Hennig 1981, Boudreaux 1987). By contrast I am using the term Insecta in a more restrictive sense (e.g. Manton 1977, Gillott 1982) to include Pterygota plus the aptergotes Diplura, Archaeognatha and Thysanura (*sensu stricto*). The sister group of the Insecta would therefore be the Parainsecta, comprising only the apterygote groups Protura, Collembola and Diplura (see Kukalovà-Peck 1987, Smith 1988; See Table 1.)

TABLE 1

SCHEME OF TEXT NOMENCLATURE INVOLVING ORDINAL, SUPRAORDINAL AND METAMORPHIC DESIGNATIONS

common name	abbreviation	order	informal supraordinal designation	metamorphic condition	major taxonomic divisions	
telsontails, proturans	(PRO)	Protura			Parainsecta (Entognatha)	HEXAPODA
springtails	(COM)	Collembola				
diplurans	(DPL)	Diplura				
bristletails	(ARC)	Archaeognatha	apterygotes	ametabolous	Insecta	
silverfish, firebrats	(TYN)	Thysanura				
mayflies	(EPH)	Ephemeroptera	palaeopterans	hemimetabolous		
dragonflies, damselflies	(ODO)	Odonata				
cockroaches	(BLA)	Blattodea	orthopteroids [Polyneoptera]			
mantises	(MAN)	Mantodea				
stick and leaf insects	(PHA)	Phasmatodea				
rock crawlers	(GRY)	Grylloblattodea				
grasshoppers, crickets	(ORT)	Orthoptera				
termites	(ISO)	Isoptera				
earwigs	(DER)	Dermaptera				
webspinners	(EMB)	Embioptera				
stoneflies	(PLE)	Plecoptera				
angel insects	(ZOR)	Zoraptera				
booklice, barklice	(PSO)	Psocoptera	hemipteroids [Paraneoptera]			
chewing lice	(MAL)	Mallophaga				
sucking lice	(ANO)	Anoplura				
cicadas, aphids, scales	(HOM)	Homoptera				
bugs	(HET)	Heteroptera				
thrips	(THY)	Thysanoptera				
alterflies, dobsonflies	(MEG)	Megaloptera	neuropteroids	holometabolous		
snakeflies	(RAP)	Raphidioptera				
lacewings, antlions	(PLA)	Planipennia				
beetles, weevils	(COL)	Coleoptera				
twisted-wing parasites	(STR)	Strepsiptera				
scorpionflies	(MEC)	Mecoptera	panorpoids			
fleas, chiggers	(SIP)	Siphonaptera				
true flies	(DIP)	Diptera				
caddisflies	(TRI)	Trichoptera				
moths, butterflies	(LEP)	Lepidoptera				
wasps, ants, bees	(HYM)	Hymenoptera				

Other common designations: dictyopteroid = Blattodea + Mantodea + Isoptera; dipteroid = Diptera + Siphonaptera: coleopteroid = Coleoptera + Strepsiptera; neuropteroid = Megaloptera + Raphidoptera + Planipennia; Endopterygota = Holometabola.

and Bitsch 1973 and Smith 1985 for summaries and various studies demonstrating relationships between general mouthpart condition and diet (Uvarov 1928, Brues 1972, Wigglesworth 1964, Cummins 1973, Wallace and Merritt 1980), then in principle a comprehensive synthesis of insect mouthpart type and diet can be made.

This study has approached this task in a twofold fashion, of which only the first phase is reported in this chapter. The first phase is an analysis of the basic phenetic patterns of hexapod mouthpart structure, using a multivariate cluster analysis of 1365 hexapod species, each with descriptions of mouthpart form and structure documented from the literature. Forty-nine variables, each which reveals some aspect of mouthpart or mouthpart related structure, were used to describe each of the 1365 hexapod species. The resulting mouthpart categorization was then expressed in phenetic dendrograms showing major and minor mouthpart groupings. In the second phase of this study, I compared the derived groupings of mouthpart structure in terms of the diets of their constituent species, ascertaining major associations between mouthpart type and diet type.

The dominant theme of the first phase of this study is the phenetic basis of the mouthpart taxonomy and the nature and pattern of the derived classification. The classification presented herein is based on morphological data and uses phenetic classification for its derivation. It is methodologically blind with respect to phylogenetic context of the included taxa. However, among some groupings of mouthpart structure there is an indirect, occasionally strong association between mouthpart type and larger systematic grouping (usually superfamily, suborder or order). Nevertheless, maintaining a methodological independence between mouthpart type and included systematic group can permit a contrast between morphogenetic change and phylogenetic evolution. For example, there may be instances wherein structural innovation has been static in the face of considerable phylogenetic turnover.

A test of the results obtained from this study is a functional morphological rationalization of the discrete mouthpart classes. In other words, apart from their pure structural distinctions, do the mouthpart classes also exhibit important, discrete differences in the way they operate? If they do, then particular key innovations can be sought to determine the fundamentally distinctive mechanisms of obtaining food. Two major approaches of functional assessment are to use biomechanical principles that link structure to function (Cowen 1979), or, alternatively, to focus on the constructional morphology of the structure and establish a qualitative understanding of how it operates (Thomas 1979). These approaches will be discussed in Chapter 3.

The results of this study are a first step in the realization of (i) a structural classification of modern hexapod mouthparts, (ii) the association between mouthpart type and diet and (iii) the geochronologic history of mouthpart type and diet. Thus the results described herein are preliminary and will require further and more detailed analysis to elucidate finer-grained patterns of mouthpart form and mouthpart/diet associations in time and space.

CHAPTER 2

JUSTIFICATION AND GOALS OF THIS STUDY

> Arthropods, especially the insects, exert a commanding presence in the dynamic processes which maintain our ecosystems. They dispose of dead vegetation, animal corpses and dung. Insects are the major herbivores. In all of these roles arthropods process and return vast amounts of nutrients to the soil. As pollinators of flowers, insects are vital links in the cycle of plant generations. And it is daunting to realize that ants and termites of the Amazon Basin account for one-third of the region's total animal biomass--and that includes tapirs, capybaras and people too! (O'Toole 1986: vi).

Because of the overwhelming dominance and importance of hexapods in land- and freshwater-based ecosystems, I have chosen hexapods as the subject of this mouthpart study. In this section I will first establish the fundamental significance of using hexapods as animals for mouthpart research and will provide reasons for why they are ideally suited for a study of gross morphology. I will then justify the use of mouthparts as an appropriate structure for analysis by mentioning their structural uniqueness and modification for diverse functions. Later, I will state my approach for an examination and evaluation of mouthpart form in hexapods, citing five advantages of proceeding with such a nontraditional study. Finally, I will discuss the goals and fundamental biological questions posed by this study.

Undoubtedly arthropods in general and insects in particular have become a prominent and ubiquitous component of terrestrial, freshwater and even marginal-marine ecosystems (see O'Toole's quote above). It has been asserted that vascular plants, hexapods and vertebrates fundamentally structure terrestrial communities (Niklas 1986) and vascular plants and hexapods provide three dominant trophic roles found in their assembly: producers, primary consumers (herbivores), secondary consumers (carnivores) and decomposers. (It should be noted that vertebrates are additionally important primary and secondary consumers in many situations.) Although this dominance can be expressed in many ways, I have selected six salient and ubiquitous features to evaluate hexapod importance. These indicators are taxonomic diversity, biomass, dietary breadth, biogeographic distribution, habitat partitioning and geologic duration. It is essential to recognize that these indicators are of fundamental importance for establishing any widespread implications derived from a study of hexapod mouthparts.

1. *Taxonomic diversity.* Both absolute measures and theoretical maxima of insect species diversity indicate that hexapods are probably the single most diverse group, at the class level, ever to inhabit the earth. Numbers of described and known species currently total approximately 875,000 (Appendix D) and, based on the number of species descriptions per unit time for various groups, there is every indication that this value will increase dramatically for most groups (Strong et al. 1984). Furthermore, while controversial, independent evidence from insect species diversity found in a single Panamanian tree species indicates that, when extended to the the diversity of the biosphere, approximately 30 million species of insects exist (Erwin 1982).

2. *Biomass.* Approximate estimates of biomass per square meter of major taxonomic groups in six major terrestrial biomes indicate that

hexapods are rarely the dominant group, and are almost always surpassed by oligochaete biomass (Little 1983). Significantly, hexapods possess the greatest biomass in desert biomes, and rank second, after oligochaetes, in tundra, temperate deciduous forest and temperate grassland. Hexapods rank third in northern coniferous forest, after oligochaetes and arachnids, and place fourth in tropical forests, after oligochaetes, gastropods and amphipods. The occurrence of amphipods as a major fraction of terrestrial animal biomass is largely confined to the southern hemisphere (Cloudsley-Thompson 1988).

3. *Dietary breadth.* Hexapod diets are collectively the most eclectic of any major organismic group; they consume virtually any nutrionally-rewarding substrate. Their dietary breadth extends not only from participating in all major dietary categories, but also in intricate partitioning of these major categories into diets characterized by monophagy on a particular host, or even a particular host region.

A further indication of insect dietary breadth is provided by anecdotal data on the exceptional diets of some species, including forms feeding on hair and feathers, sponges, bacteria in petroleum, urine, textile fibers, wax, wood and various salt solutions (Uvarov 1928, Brues 1972). Typical foods include freshwater plankton, decaying plant and animal tissue, live animal tissue including blood, and all major plant organs and their tissues--particularly roots, wood, sap, leaves, flowers, nectar, pollen and seeds. While the taxonomically comparable vertebrates rival insects in dietary breadth, there are several food resources that are excluded, since no forms subsist exclusively on wood, hair and feathers, textile fibers, wax and decaying plant material.

4. *Biogeographic distribution.* Insects occur in all regions of the biosphere except at the polar extremities and the deeper oceanic areas. With regard to biogeographic distribution, the only glaring exception is the submarine realm, although several hundred hexapods are considered marine, including caddisfly nymphs in sea urchins, seal lice, chrysomelid beetle larvae on the eelgrass *Zostera* and the marine water-strider *Halobates* found on the surface of oceans several hundred miles from land (see Cheng 1976). The intertidal and supratidal zones are richly populated with marginally marine forms, including bristletails, beetles, flies and other groups. On land, collembolans occur up to 6000m (Swan 1961); stonefly nymphs and fly larvae inhabit artesian water channels that are found in boreholes (Stanford and Ward 1988); and diurnally active beetles inhabit land surfaces with temperatures up to 51°C (Roer 1975). Hexapods have succesfully colonized all desert habitats and many groups have developed unique xeric adaptations (Cloudsley-Thompson 1988). Although most prolific in the tropics, hexapods nevertheless occur in profusion on all land masses except at the highest altitudes.

5. *Habitat partitioning* The myriad ways that hexapods have partitioned the biosphere is astonishing (see Southwood 1978). Although only a brief synopsis can be presented, hexapods have invaded every major habitat in freshwater and on land. Much of this success involves the "dissociation in form and structure between the feeding and growing stages [=immatures] and the distributive and reproductive stages [=adults]" (Hinton 1977: 81, insertions mine). In fresh water, there are larval and adult filterers, scrapers, collectors, herbivores and

carnivores (Merritt and Cummins 1984) that trophically link producers with higher-level vertebrate carnivores. On land, insects have evolved several special strategies for using plants simultaneously as food resources and domiciles. These include external foliage feeding, wood-boring, leaf- and root-galling and leaf- mining, each of which is characterized by a wide spectrum of microhabitats. Wood-boring forms, for example, can specialize in live, recently dead, decomposing, and highly decomposed phases, complicated by occurrence in particular anatomical regions of the wood (Hamilton 1978). Predaceous forms often specialize on particular taxonomic groups whereas parasitic and parasitoidic forms often are host-specific and tissue-specific (Vinson and Barbosa 1987). Other special habitats, each with a variety of spatio-temporally discrete microhabitats, are carrion, vertebrate feces, macro-fungal sporocarps and even house-borne dustballs.

6. *Geochronologic Duration*. Although relative latecomers when compared to other major class-level taxa, hexapods have their earliest occurrence in the Early Devonian (Hirst and Maulik 1926, Labandeira et al. 1988) about 400 million years ago, and by Late Carboniferous times, 320Ma, they were already the dominant terrestrial and probably freshwater animal group. (Nothing is known of the approximately 55 my gap between the Middle Devonian and earliest Late Carboniferous.) Patterns of familial- and ordinal-level diversity indicate moderate expansion during the late Paleozoic, followed by a Late Permian extinction of archaic orders, after which a spectacular diversification ensued during the later Mesozoic and Cenozoic (Sepkoski and Hulver 1985), partly in concert with the appearance of flowering plants (Tiffney 1981). Many

modern, mostly anthophilous families were established by the Cretaceous (Willemstein 1987), and by Baltic Amber times about 38Ma, the insect fauna was demonstrably modern at the familial level, with many genera and occasional species still extant (Larsson 1978, Whalley 1988). Insects appear to have been unaffected by the Cretaceous extinctions (Briggs et al. 1988, Whalley 1988). Since their dominance of terrestrial habitats certainly by Late Carboniferous times, all evidence indicates that insects have been the dominant and most diverse animal group.

By most of the above critera, it has been established that insects constitute the dominant animal group on land and probably in freshwater. This pre-eminence can be documented for their taxonomic diversity, marginally for their biomass, probably for their dietary breadth, and certainly for biogeographic distribution and habitat partitioning: they have an impressive geologic longevity. This conclusion begs the question: Why have insects achieved such a predominant role in freshwater and terrestrial ecosystems?

This question is approachable by consideration of those features of insect design that may account for such dominance. If we examine those basic functions that insects share with all other animals, two prominent functions come to mind--feeding and reproduction. Other features that taxonomically are more restricted among animals include presence of an exoskeleton, flight and developmental metamorphosis. With regard to reproduction, the male aedeagus and the female ovipositor are the relevant structures. Both structures possess amazing diversity of form within lower taxonomic levels--diversity that is essential for establishing species-level distinctions in most groups. While the ovipositor is highly variable within hexapods and contains several paired elements used for transferal of eggs from the ovaries to an appropriate substrate, it nevertheless lacks diverse, classwide structural complexity. By contrast, structures involved with feeding are an anterior-posterior series of mouthparts, each pair of which often bear numerous independent elements. Whereas the exoskeleton consists of numerous sclerites that range variously in size, shape and juxtaposition, their overall structure within hexapods is highly stereotyped. Similarly wings are highly uniform and consist of general trends in vein reduction, variations in shape and size and wing number. (A few recent studies indicate that there may be four or five biomechanically distinctive ways that insect use wings in flight [Wootton 1988, Ellington 1988].) Although metamorphosis has profound implications for the structure of immature and adult insects, it is not clear how an overall measure of "metamorphic form" can be achieved in many externally featureless larvae, whose only visible structural complexity often is the mouthparts. In conclusion, the most complex, variable and potentially informative structure or structure-complex that insects bear which may potentially inform us about the "Why" question above is mouthparts. Other relevant structure-complexes either have a high degree of stereotypy among higher taxonomic levels or they are operationally difficult to assess. Structural stereotypy makes morphological analyses of major trends among groups less attractive for answering basic issues of insect form. By contrast, Metcalf expressed the structural complexity of insect mouthparts in the following way:

> Probably no group of structures in the animal kingdom exhibits a better example of the adaptive modification of originally similar, serially arranged organs to very different-looking structures and to diverse functions... It will be seen that these structures diversify to such an extent that their homologies would never be suspected; and can be recognized, if at all, only by the most judicious study of their embryonic and postembryonic development (Metcalf 1929: 110, 111).

The question of why insects have achieved an overwhelming representation in freshwater and especially terrestrial habitats is important and fundamental not only to entomologists, but also for biologists who seek to understand the evolution of freshwater and terrestrial ecosystem structure. Using the structural diversity of hexapod mouthparts to characterize this dominance can be approached by several traditional and nontraditional ways.

Traditional approaches of inquiry have focused primarily on systematic studies, characterized by the establishment of the taxonomic identities and relationships of particular insect groups. In these studies morphological variation, as it relates to function, ecology or other primarily nontaxonomic aspects, is usually only briefly discussed. Other approaches toward the study of form are to understand the genotype (genetics), or the ontogeny of structure (embryology), or to evaluate form directly (morphology). Unfortunately, knowledge about the genetics and embryology from a representative sample of insects--a sample that would minimally require several hundred characterizations for the purposes of this study--is not available, even if it were possible to causally link knowledge of the genotype and development to its expression on the phenotype. This leaves gross, or phenotypic, morphology as the only viable alternative available for a study of insect mouthparts.

Although there is an extensive literature documenting mouthpart structure and thus providing a vast source of raw data for this study, there are also the following advantages that the study of mouthpart structure proposed herein can provide.

1. *Overall Philosophic Approach.* The approach taken in this study emphasizes the elucidation of pure morphology for characterizing hexapod mouthpart structure. While most recent investigations of insect morphology are done with an *a priori* goal of determining systematic relationships of the taxa under consideration, this study is primarily concerned with determining hexapod morphology as it exists, without reference to taxonomy or phylogeny. Thus this analysis of hexapod mouthparts uses an unconventional method rarely undertaken in recent entomological studies.

2. *Taxonomic scope.* The diversity of hexapod taxa examined in this study includes genera from all 34 orders and 70% of of all families; it represents 1365 separate data-entries (see Section 6.1 for specifics). The coverage is fine-grained enough to capture major and intermediate-level trends in mouthpart structure. Notably, virtually all previous treatments of mouthpart structure have been either undertaken at the level of overly broad, generalized *Gestalten*, such as those found in textbooks (e.g. Borror et al. 1976; Gillott 1980), or analyses of single or a few representatives of major structural categories (Snodgrass 1928, 1935), or confined to analyses of single families or lower taxa (Bugnion 1930, Nel and DeVilliers 1988), wherein most differences in mouthpart structure are insignificant when compared to the total diversity of mouthpart structure among all hexapods. Although

a few, occasional studies have aimed at the general level desired in this study (Metcalf 1929, Chaudonneret 1982-89), their analytic context was couched in *a priori* taxonomic considerations. This study is the first purely phenetic, comprehensive analysis of hexapod mouthpart structure.

3. *Morphological context*. The centrality and omnipresence of mouthparts is a structural expression of hexapodan life-habits. Feeding and, by extension mouthparts, are probably more important than flight, locomotion, and at least for immatures, reproduction; no other structural feature probably affects the daily lives of hexapods as much as mouthparts. It should be noted that of all the major structures borne by insects that interact directly with the environment--mouthparts, wings, legs, ovipositor, gills, etc.--mouthparts are the most universal and, unlike the other mentioned structures, occur in virtually all species. Since feeding is both fundamental and diverse in hexapods, the potential opportunity for structural modification of mouthparts is immense. Consequently, hexapodan mouthparts present an ideal structural complex for the analysis of gross structural variation and its association with hexapodan life-habits.

4. *Macroevolutionary biology*. There are several implications of this study for the macroevolutionary biology of hexapods. First, within Recent hexapods, an examination of the degree of phylogenetic convergence on the same mouthpart type can provide insight into the multiple occupation of food niches by taxonomically disparate lineages. This is achieved by evaluating the taxonomic membership of mouthpart classes and recording the number of independent lineages present in that class.

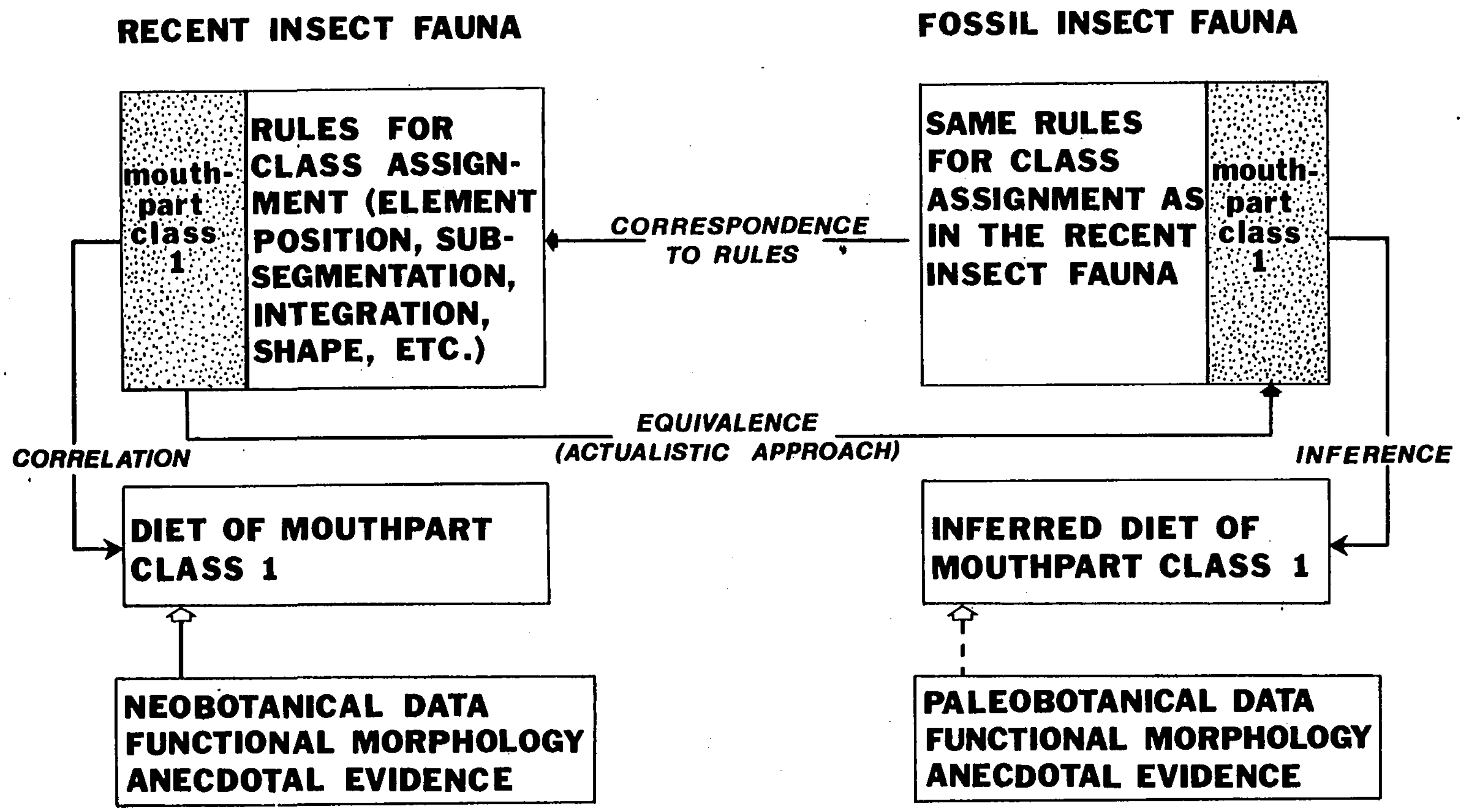
Secondly, a subsidiary examination of the geochronologic record of mouthpart types documented by evidence from the fossil record and phylogenetic analyses can provide a record of the first known appearance and historical trends of mouthpart types and their constituent taxa during the past 400 million years. Lastly, when mouthpart type is associated with diet (Phases 1 and 2 of this study), an indication of the origin, evolution and recent structure of feeding guilds (sensu Root 1973) can be established, especially with respect to the expansion and contraction of food resources and the concomitant opportunism showed by mouthpart types toward the exploitation of a given food resource. In other words: What has been the response of mouthpart form to the evolving biota? Has this response resulted in an increase in the number of fundamental mouthpart types and resulted in a finer partitioning of available food resources?

5. *Comparison with analogous arthropod groups.* Four major arthropod groups have invaded the terrestrial realm: crustaceans, arachnids, myriapods and hexapods (Labandeira and Beall 1990). Of these, only hexapods have partitioned their food resource world to include all conceivable nutritional categories. Concomitantly, only insects exhibit a bewildering variation of mouthpart structure. While crustaceans exhibit complex specializations for chewing, filter-feeding and piercing-and-sucking (Schram 1986), terrestrial members are only "mandibulate" chewers. Nonacariform arachnids have highly stereotyped mouthparts comprising only two pairs of mouthparts--a pair of anterior fang-like chelicerae and a posterior pair of chelate or palpiform pedipalps. According to Snodgrass (1948), early arachnids lacked true

jaws and subsequently have been channeled into liquid-feeding. However, dominantly parasitic mites and ticks have developed a few interesting mouthpart modifications, including specializations for rasping, piercing and even siphoning (James and Harwood 1969). Myriapods, by contrast, possess greater mouthpart complexity and bear analogs to the labral, mandibular, maxillary and often labial regions of hexapods, but all myriapod forms are fundamentally phytophagous or raptorial chewers and lack the fluid-feeding specializations of hexapods. Of these four terrestrial arthropod groups, the crustaceans probably did not invade the terrestrial realm until the late Mesozoic (Little 1983); the three other groups date back to the Paleozoic, but only insects have invaded, in entirety, the vast dietary spectrum found in terrestrial ecosystems.

The goals of this study are simply to ascertain objectively the number, diversity and systematic membership of major mouthpart groupings (or fundamental mouthpart "body-plans") in the Recent insect fauna. A second goal is the establishment of a model of mouthpart/diet association that can be used to infer diets of Recent species where dietary information is often unknown or very poor, or of fossil species where paleobotanical dietary data are frequently unavailable but mouthpart structure is present. The mouthpart/diet association model can also be used to examine the proportional representation of insect mouthpart groupings and dietary associations in selected, well-preserved fossil insect deposits or in recent terrestrial communities (Table 2). The third goal of this study is to document from the fossil record the historical pattern of mouthpart classs and their associated diets.

TABLE 2. Model for application of Recent mouthpart classes to the fossil record.


RECENT INSECT FAUNA
FOSSIL INSECT FAUNA
mouth-part class 1
RULES FOR CLASS ASSIGNMENT (ELEMENT POSITION, SUB-SEGMENTATION, INTEGRATION, SHAPE, ETC.)
CORRESPONDENCE TO RULES
SAME RULES FOR CLASS ASSIGNMENT AS IN THE RECENT INSECT FAUNA
mouth-part class 1
EQUIVALENCE (ACTUALISTIC APPROACH)
CORRELATION
INFERENCE
DIET OF MOUTHPART CLASS 1
INFERRED DIET OF MOUTHPART CLASS 1
NEOBOTANICAL DATA
FUNCTIONAL MORPHOLOGY
ANECDOTAL EVIDENCE
PALEOBOTANICAL DATA
FUNCTIONAL MORPHOLOGY
ANECDOTAL EVIDENCE

Although fundamental questions in biology are often simple, they nevertheless provide excellent vehicles for understanding large-scale patterns of a group in time and space. The fundamental questions posed by this study are: "What are and why are there so many discrete modifications of hexapod mouthparts?", "What is their relationship to diet?", and "How may they inform us about the geochronological evolution of feeding guilds in hexapods?" The diversities of mouthpart structures and of feeding guilds are undoubtedly strongly associated. Once a pattern is documented, this association can be used to establish, with data from the fossil record and phylogenetic studies, a record of the expansion of hexapod feeding styles from inconspicuous primitive forms on primitive vascular plants during the Devonian, to the unbridled wealth of feeding styles today.

CHAPTER 3

PREVIOUS RESEARCH

The number of studies of insect mouthpart morphology is vast, numbering at least two to three thousand (approximately 1200 references have been consulted for the data presented herein). Among this wealth of literature, the overwhelming majority of studies are descriptive accounts of selected insect species; a few are syntheses of previous studies (e.g. Berlese 1909; Snodgrass 1924, 1944; Matsuda 1965; Gouin 1968) that take a taxonomic approach to mouthpart structure contrasting similarities and differences of structure among representatives of various insect orders. A minor portion of the literature, most of it recent, discusses the evolutionary implications of mouthpart patterns (e.g., Manton 1964, 1979; Kristensen 1984; Ashe 1984a, 1984b), or the roles of mouthpart types in feeding guilds (e.g. Balduf 1935, Wallace and Merritt 1980, Cummins and Merritt 1984, Caltagirone 1984). In this section two approaches are used to distill this profusion of literature --the first describes the historical development of mouthpart research by national region and the second emphasizes recent trends in the functional morphology of insect mouthparts.

3.1. A Brief Overview of Mouthpart-Morphology Research

Although insect-mouthpart investigations can be traced with assurance to the natural history observations in Aristotle's *De Partibus*

Animalium and probably to the ancient Egyptians by their anatomically accurate renderings of mouthparts in models of sacred scarabs, the modern era of mouthpart research did not commence until the late 1700's and early 1800's. Such early publications as Clairville's *Helvetische Entomologie* (1798-1806) in fact used mouthpart structure to separate common insect orders into two major groups (his "tribes")--the Mandibulata with chewing mouthparts and the Haustellata, with sucking mouthparts. This practice--of using mouthpart type as one of a few, major, diagnostic characters for insect classification at ordinal level--continued into such later works as Lubbock's *On the Origin and Metamorphosis of Insects* (1890) and *The Cambridge Natural History* (Sharp 1922: 172). (See Frost [1959] for an anatomical extension of this idea.) During the 1850's to 1900's, mostly German and to a lesser degree British and American, anatomists published articles detailing the microscopic structure of mouthparts from various common insects.

During the early part of the Twentieth Century, the momentum of insect mouthpart research shifted to the United States. This momentum was evidenced initially by such eminent systematic entomologists as A.S. Packard (fl. 1890's), V.L. Kellogg (fl. 1890's to 1900's) and J.W. Folsom (fl. 1900's), and later by the pioneering work of R.E. Snodgrass (fl. 1900's to 1960's), a comparative morphologist affiliated with the Bureau of Entomology of the Department of Agriculture. Snodgrass had a major influence on American insect morphology, popularizing a theory of head segmentation proposed earlier by German morphologists (Rempel 1975) and establishing a much-used framework for recognition of mouthpart structure homologies across all insect orders. Other major researchers of this period were A. Peterson (fl. 1910's to 1950's) of Ohio State University and G.C. Crampton (fl. 1910's to 1940's) of the University of Massachusetts, both of whom contributed toward an understanding of general mouthpart structure across all insect orders. Crampton, in particular, introduced comparative morphologic studies of a particular mouthpart structure, discussing and illustrating major variations in form occurring among all insect orders. Up to that time the tradition was to describe mouthparts as an ensemble of a single species, generally with minimal reference to interelement variation among related or unrelated taxa.

During the 1920's to 1950's a separate school of insect morphology was established at Stanford University by G.W. Ferris (Rempel 1975). The Stanford School produced a host of articles on mouthpart-morphology published by their in-house publication, *Microentomology*: these articles were often at odds with Snodgrass's interpretation of homologies of mouthparts and other head-related structures (Matsuda 1965). Meanwhile, at the Cornell University Agricultural Experiment Station, affiliated with the premier entomology department in North America, several studies of mouthpart morphology were produced (Johannsen 1943; Butt 1943, 1951; Kelsey 1954). By the later 1960's the "classic period" of descriptive mouthpart-morphology in North America was waning; most of these studies were synthesized by Matsuda (1965) in his monograph, *Morphology and Evolution of the Insect Head*. The tradition of descriptive morphology using light microscopy and line drawings became supplanted by more functionally oriented studies, often at higher magnifications and using electron microscopy.

Meanwhile in Europe three distinct schools of mouthpart research were producing a prolific literature. The earliest was in Germany, began by H. Weber (fl. 1920's to 1930's), principally at the Zoology Institute of the University of Tübingen (Matsuda 1965), who spawned many students that produced monographic publications on common or interesting species. Most of these monographs (e.g. Wundt 1961, Mickoleit 1963, Ramcke 1965) were published in *Zoologische Jahrbücher* and possessed the imprint of the *Konstruktionsmorphologie* tradition, stressing the head and mouthpart ground-plan of the examined insects and including functionally interpretative accounts of the structures studied.

Later, in France, at the Department of Zoology at the University of Dijon, J. Chaudonneret established a school of descriptive morphology and embryology during the 1940's to 1970's (Rempel 1975). Some of his students published their mouthpart morphology studies locally in the *Travaux Laboratoire de Zoologie et de Station Aquicole Grimaldi de la Faculté des Sciences de Dijon* (e.g. Bitsch 1952, Moulins 1959, Jaboulet 1960). Recently, Chaudonneret has published a series of articles on the central structural theme of the insect head and mouthparts (1982), followed by major variations of this theme found in various insect groups (1983-1989). Though stressing both phylogenetic and functional-morphological approaches in this extended study, many of Chaudonneret's mouthpart/head groupings are similar to groupings of this study.

Lastly, there was a more diffuse British school of mouthpart morphology, largely centered at the University of Manchester (E.J. Popham, fl. 1960's and 1970's; M.E.G. Evans and T.G. Forsythe, fl. 1980's), the University of Bristol (D.G. Pollard, fl. 1950's to 1970's), University of Aberdeen, (J.R.T. Short, fl. 1950's) and the British Museum of Natural History (B. Jobling, fl. 1920's and 1930's; S.M. Manton, fl. 1960's and 1970's). Among these British researchers there was a tendency to stress the functional as well as the descriptive aspects of mouthpart morphology, of which S.M. Manton's ideas were perhaps the most controversial (Gupta 1979), with her suggestion that mouthparts and other major structures arose independently several times within the insects (Manton 1977, 1979). In general, the "classic period" of European mouthpart morphology, as in North America, became replaced by ultrastructural studies employing electron microscopy. However, during the 1970's and 1980's, occasional monographical works of insect mouthparts in the classical vein have appeared in *Zoologische Jahrbücher* by the German School (e.g. Honomichl 1975, Hirsch 1986).

The British influence in India generated an interest in applied entomological research, much of it devoted to the protection of subtropical crops and the control of human diseases transmitted by insect vectors. As early as the 1910's there was research into the mouthpart structure of bothersome Diptera (Cragg 1912a to 1913c), and later there was extensive research into the control of various agricultural pests (Ahmad 1943, Kumari 1955, Akbar 1957, Puri 1958). Many descriptive mouthpart-morphology reports from these studies often detailed the mouthpart structure of insect taxa absent in North America or Europe.

3.2. Studies Focusing on the Functional Morphology of Hexapod Mouthparts

In the broadest sense of the term, functional morphology can be categorized into three approaches, in terms of both historical development of a given discipline and in terms of increasing scientific rigor. These are (i) natural history observations, whereby some ecologic/ organismic association is made, such as mouthpart type and diet, without resort to an analysis of causality; (ii) a form-and-function analysis, whereby some descriptive aspect of an organism's structure is used to causally explain a relevant organismic process, such as mandibular dentition accounting for processing of a particular food type; and (iii) biomechanical modelling, wherein some feature of anatomy is characterized such that a biological function of the same feature can be explained, often mathematically, in terms of a cost/benefit explanation, assuming an adaptationist paradigm. This third approach focuses on a particular mechanism and seeks to explain how a structure works. When the vast insect mouthpart and diet literature is considered, functional-morphological studies have been relatively infrequent. The relevant literature that does discuss mouthpart morphology and diet uses the first approach most often and the second approach is infrequently used. Snodgrass (1935) however was an exception, summarizing much of what was known about the structure of major mouthpart types and how they worked. His contributions were valuable not only in his systmatization of descriptive morphology--then in a morass of terminological confusion--but also in his illustration of how "morphology must be intimate with function" (1935: 1). Notably, Chaudonneret has continued this tradition in a series of publications detailing the *Baupläne* of the insect head and its principal modifications in insect taxa (1966, 1982-1989).

Although historically the third approach rarely has been used, it has been applied since the early 1970's to a few relatively well-constrained, mostly liquid- or particle-feeding, mouthpart complexes. These include: the strike mechanism of the labial mask in larval odonatans (Caillère 1972, Pritchard 1976, Tanaka and Hisada 1980), the neurosensory and structural basis of host-selection and monitoring of liquid-feeding in the hemipteran beak (Backus 1985, 1987, 1988; Backus and McLean 1985), the protraction/retraction mechanism of the cyclorrhaphan dipteran labellum (Thomson 1977, van der Starre 1977, van der Starre and Ruigrok 1980), and the proboscis protraction/retraction and pumping mechanisms in adult lepidopterans (Eastham and Eassa 1955, Hepburn 1971, Bänziger 1971, Kingsolver and Daniel 1979). However, considerable attention has recently been devoted to the biomechanics of suspension feeding systems in larval nematoceran dipterans and to a lesser degree, in trichopteran and ephemeropteran naiads. The development of a body of theory outlining possible passive and active mechanisms for suspended particle capture (Rubenstein and Koehl 1977; LaBarbera 1978, 1984), largely from examples from the marine realm, has prompted examination of some aquatic, filter-feeding insects. These studies have concentrated on (i) the relationship of mouthpart vestiture to trapped particle size and fluid dynamics, (ii) the designation of spatially-based mouthpart units, either informally or formally, to establish flow-creation, particle-interception and particle-retention ensembles of mouthpart elements and (iii) elucidation of temporally-based mouthpart systems, whose sequential deployment results in creation of appropriate current structure for the trapping and securing of particles (Braimah 1987a, 1987b; Merritt and Craig 1987; Dahl et al. 1988). Techniques for functional inference are principally cine films for behavioral documentation, scanning electron microscopy for determination of often ultrafine mouthpart vestiture, and functional analysis of mouthpart musculation and associated movement (Tanaka and Hisada 1980, Craig and Chance 1982, Giguère and Dill 1983; see Smith [1985] for a review of the above-mentioned and other examples.)

CHAPTER 4

INSECT MOUTHPART STRUCTURE AND RELATED ISSUES

Since insect mouthparts consist of characteristic structures occurring on specified head segments, each of which are fundamentally represented in virtually all major groups of insects, a general discussion of insect head segmentation is an appropriate context for introducing a descriptive account of mouthpart structure. I will then briefly note the problems of homologizing mouthpart structure within the class. Finally, I will provide a discussion of mouthpart structure in generalized forms, which is the primitive condition for all insects, and will finish with examples of deviation from the generalized condition.

4.1. Insect Head Segmentation

Perhaps no other aspect of insect anatomy has engendered as much controversy as the number and identification of head segments (Gillott 1982). The debate originated by embryologists during the 1900's (e.g. Folsom 1900, Heymons 1901, Borner 1909, Hoffman 1911) who proposed various numbers of head segments, principally in apterygotes, and identified these segments with particular coelomic sacs or embryonic ganglionic masses (neuromeres). Later during the century, morphological and embryological studies extended the enumeration and characterization of head segments to pterygotes, including milkweed bugs (Butt 1949), earwigs (Lhoste 1951) and stick-insects (Bitsch 1963). By that time some of the claims of the earlier workers were reversed, including the unreliability of using hypopharyngeal coelomic cavities to demarcate segment presence (Anderson 1959), and the absence of any "superlingual segment" since superlingulae were later demonstrated to have a mandibular origin (Tiegs 1940).

Although there are currently more disagreements than agreements regarding insect head segmentation, the situation is probably more resolved than any time during the recent past. Several items still elude an acceptable solution, namely (i) the definitive presence of an acron homologous to the prostomium of annelids, (ii) the presence of a "labral segment" and whether it bears a labrum that may or may not be appendicular and bilobed in structure, (iii) the presence of an antennal segment and the related issue of whether antennae are true appendages that are homologous to a generalized limb and (iv) identification of the "intercalary segment" (or "premandibular segment") and, if it exists, whether it contributes tissue to head or mouthpart formation. On a brighter note, several patterns of head segmentation have widespread agreement. First, virtually all researchers agree on the existence of the posteriormost three segments of the insect head--the gnathal segments of the mandible, maxilla and labium. Second, among embryologists, the total number of segments hovers at either six or seven. (Researchers using external structure as a criterion posit a segmentation number with much more variability, ranging from three to nine according to Matsuda [1965] or three to seven according to Rempel [1975] and Gillott [1980].) Lastly, it appears that, with few exceptions (e.g. Chaudonneret 1960), most embryologists and morphologists assess the number of cephalic neuromeres at six. The first three neuromeres comprise the brain and the last three are termed the subesophageal ganglion, which contains ganglionic regions, each associated with a gnathal segment.

The major message of a near-century of extensive embryological and morphological research on a very diverse and phenotypically plastic group of arthropods is that the insect head probably has six segments (Matsuda 1965, Rempel 1975)--specifically (i) the preantennal segment bearing the eyes and containing the protocerebrum, (ii) the antennal segment bearing the antennae and including the deutocerebrum, (iii) the relatively reduced intercalary (premandibular) segment, bearing probably the epipharynx and having the tritocerebrum as its neuromere, (iv) the mandibular segment, bearing the mandibles and consisting of the anterior region of the subesophageal ganglion, (v) the maxillary segment, bearing the maxillary appendages and consisting of the medial region of the subesophageal ganglion and lastly (vi) the labial segment, bearing the labial appendages, including perhaps the gula, with its neuromere localized at the posterior part of the subesophageal ganglion. It appears that a major issue is whether the preantennal segment is independent of the acron (clypeolabral segment) or is lost (cf. Matsuda 1965 with Rempel 1975; Richards and Davies 1977). If the two are recognizably separate, then true head segmentation would number seven (Snodgrass 1960, Denis and Bitsch 1973).

4.2. The Problem of Homology

Embryological, morphological and paleontological evidence indicates that at least the gnathal mouthpart appendages are serially homologous to a generalized insect walking limb (Snodgrass 1935, Chapman 1982; Kukalová-Peck 1985, 1987). This homology is best evident in some fossil insect material from the Early Pennsylvanian (Kukalová-Peck 1985, 1987) or from the maxillary palps of certain extant apterygote insects (Sharov 1966). The palpus/walking limb homology is based on appendage position, appendage segment number, internal and independent musculation of each appendage segment, and other features.

Although the palpus/walking limb homology appears straight-forward, there are several difficulties in recognizing homology in other, less discernible mouthpart regions. Traditional morphological description and analysis, which is the approach taken by researchers describing adult insect mouthparts, often with little or no embryological or paleontological evidence available, uses position, musculation and innervation of head and mouthpart sclerites for their identification. Nevertheless, it is a common phenomenon for muscles to shift their regions of attachment, often at a differential rate with respect to adjacent sclerites and muscles (DuPorte 1946, Evans 1961, Matsuda 1965). Use of motor innervation for determining sclerite homology has a similar liability since motor nerves contain fibers that frequently have origins from more than one embryologic region, in many tax incorporating elements from nearby segments in many forms (Chapman 1982, p. 616). Because of these uncertainities, embryology serves as the single best criterion for determining sclerite or appendage homology (Matsuda 1965, but see DuPorte 1957 for a contrary view). However, embryological studies have documented the development of only a few, widely-cited insects cannot address problems of comparative morphology of most adult insects described in the mouthpart literature. Consequently the dilemma remains: although many researchers tacitly agree on the homologies of insect mouthparts and head sclerites based on several lines of suggestive, albeit imperfect evidence, only in a small portion of the total pool of insects characterized by mouthpart descriptions can mouthpart elements be reasonably traced to embryological *anlagen*.

This study, based principally on external macrostructure, does not assume phylogenetic or structural homology among analogous structures that function in the same or similar way. In most instances this structural analogy will correspond to a structural homology. In some cases there is convincing evidence that the structurally and functionally similar structures compared are not homologous--e.g. the mouthhooks ("mandibles") of higher dipteran larvae and the mandibles of generalized adult insects (Snodgrass 1935, Cook 1949, Bitsch and Denis 1973, but also see Ludwig 1949 and Teskey 1981 for a contrasting view). The presence of analogous but not necessarily homologous mouthpart elements in this database is completely appropriate, even preferable, for the goals of this study. The major impetus of this study is to assess the fundamental modes by which recent insect mouthparts are morphologically deployed, irrespective of phylogeny. Morphological and functional convergence in mouthparts of insects belonging to phylogenetically disparate groups can be a strong statement regarding the ecological or evolutionary success of particular, recurring mouthpart types.

4.3. General Insect Mouthpart Structure

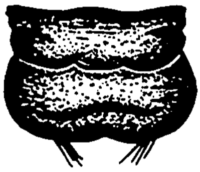
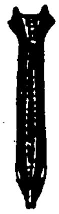
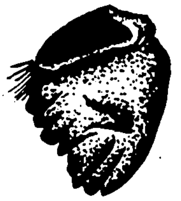
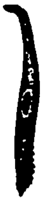
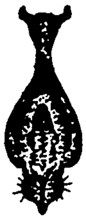
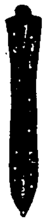
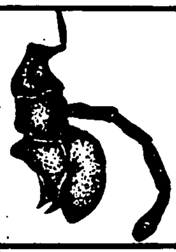
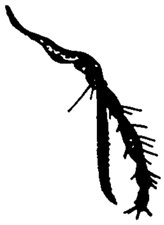
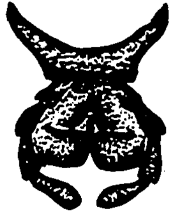
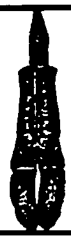
I am defining insect mouthparts as comprising all external, flexed or otherwise movable elements of the head, exclusive of dorsal sensory organs, that occur on the anatomical ventrum of the head. Insect mouthparts consist of five groups of elements--namely the labrum-epipharynx, mandibles, hypopharynx and associated structures, maxillae and labium--that possess the following characteristics. (1), mouthparts are arranged sequentially, circumorally and in a fixed anatomical position on the ventral region of the head, in the order enumerated above. Although generalized mouthparts are situated on the underside of the head (the hypognathous condition), corresponding to the anatomically ventral region of the primitive insect head, various modifications have altered mouthpart position on the head. Prolongation of the anterior region of the head results in anterior (prognathous) mouthparts, and the posteroventral canting of the mouthpart region results in opistognathous mouthparts. (2), mouthparts are either unpaired in the example of the labrum, some hypopharynges and the mesial region of the labium, or they are paired as exemplified by some hypopharynges, mandibles, maxillae and the lateral aspect of the labium. (Nevertheless there is embryological and paleontological evidence indicating that some functionally unpaired elements, such as the labrum, originated by mesial fusion of a pair of lateral appendages [Kukalovà-Peck 1987, Smith 1988].) (3), with the exception of the Order Thysanoptera, mouthparts are fundamentally bilaterally symmetrical at a gross level. Minor asymmetries occur occasionally for individual elements and are associated with sexual dimorphism or feeding modifications. (4), mouthparts consist either of skeletal or membranous projections of the head capsule (e.g. labrum-epipharynx) or true, embryologically derived appendages (e.g. maxillae). (5), mouthparts consist of either single elements, such as the labrum and most mandibles (some mandibles have articulating elements, such as prosthecae or laciniae mobili), or of multielements, such as the maxillae and labium, composed of unsegmented mesial projections and segmented distal palps. (6), insect mouthpart elements, either within a segmental region or among two or more segmental regions, are co-opted to produce a composite structure with a single function. Examples include the maxilla of a grasshopper (an intrasegmental multielement complex) or the beak of a cinch bug (an intersegmental multielement complex). (See Dullemeijer 1974, Chap. 8, for a theoretical treatment of multielement systems.) (7), all insect mouthparts are ultimately homologizable, albeit often with pronounced structural deviation (Metcalf 1929), from a generalized groundplan. (Table 3 summarizes the gross characteristics of insect mouthparts.)

4.4. A General Account of Mouthpart Structure

The primitive condition for insect mouthparts is the generalized mandibulate state (Frost 1959; Boudreaux 1987). This is true for apterygotes as well as pterygotes. However, two major mouthpart-related distinctions exist between the three apterygote groups and the group comprising the Thysanura and Pterygota. The former are entognathate and possess monocondylous mandibles, whereas the latter are ectognathate and bear dicondylous mandibles. One group, the Archaeognatha, occupies an intermediate condition characterized by mandibular monocondyly and

TABLE 3

SUMMARY OF GROSS CHARACTERISTICS OF HEXAPOD MOUTHPARTS

						Examples	
Mouthpart Region	***Anatomical Sequence***	***Head region or appendage***	***Paired or unpaired***	***Nature of element(s)***	***Segment Origin***	***Generalized mouthparts***	***Derived mouthparts***
labrum/ epipharynx	1 ANTERIOR	head region	unpaired	single element	labrum: ?acron epipharynx: intercalary		
mandibles	2	appendage	paired	single element (some exceptions)	mandibular		
hypopharynx	3	head region	unpaired	single element or multielement	mostly mandibular; also maxillary and labial in many forms		
maxillae	4	appendage	paired	multi-element	maxillary		
labium	5 POSTERIOR	appendage	unpared;	multi- formed by fused second maxillae	labial element		

ectognathy. These characters may have more phylogenetic importance than functional significance since, with the exception of the ability of monocondylic mandibles to slide dorsoventrally in apterygotes (Kukalová-Peck, pers. comm.), the basic feeding mechanism is quite similar between apterygote forms and primitive pterygote forms. Realizing these mouthpart distinctions, I will provide a brief account of the generalized mouthpart condition for lower pterygote (or "orthopteroid") insects (see Table 1 for informal nomenclature of hexapod groups). Some of the ensuing discussion comes from Snodgrass (1935), Matsuda (1965), Richards and Davies (1977) and Smith (1985).

4.4.1. **Labrum and Epipharynx.**

The labrum, informally termed the "upper lip," consists of an unpaired, single element (Smith 1985) that projects downward and is located anterior to the preoral cavity. It is proximally attached to the clypeus and is delimited from the clypeus by the clypeolabral suture. Although the clypeus has limited mobility, the labrum is capable of retraction, production, reduction and lateral movements (Snodgrass 1947). These motions are effected by labral muscles originating on the frontal region of the head capsule and inserted into either the proximal transverse margin of the labrum or on small, sclerified extensions occurring at the proximal lateral angles, known as tormae. Often the labrum is indistinctly to completely fused to the clypeus, forming a composite structure, the clypeolabrum (Snodgrass 1935). In forms with piercing mouthparts, the labrum either is a triangular beak brace or a stylet, often in conjunction with the epipharynx.

The epipharyngeal wall forms the internal surface of the labrum and clypeus and is subject to considerable modification. Since the epipharynx forms the anterior membranous surface of the food chamber, it is an important organ for gustation. Its surface frequently bears hairs, pectinate setae, pustulate sensillae, molariform denticles, or other processes used in food manipulation or sensation. In many forms the epipharynx serves as a tongue and is used in compressing food within the oral chamber.

4.4.2. Mandibles

Insect mandibles are paired, usually simple appendages situated lateral to the oral chamber and moved by strong mesially-directed adductor muscles necessary for comminuting food. Weaker abductor muscles are responsible for extending the mandibles abaxially in a position that can be acted on by the abductor power stroke. Adductor and abductor muscles work in opposition to each other, originating on the head capsule dorsum and inserting on apodemes located on the mesial and distal margins of the mandibular base, respectively, for efficient leverage. Apterygote mandibles exclusive of thysanurans articulate with the head capsule by one condyle only and are additionally capable of some up-and-down sliding movement (Manton 1977). By contrast, thysanuran and pterygote mandibles are dicondylous and possess strong transverse movement. Generally the abductor/adductor hinge plane, delineated by the anterior and posterior mandibular condyles, is quite long and is positioned parallel to the sagittal axis for lateral jaw movement.

Mandibular structure is characterized by a wide, usually triangular base bearing apodemes for muscular attachment and condyles for mandible/ head capsule articulation. From the proximal base, the mandible tapers distally to one or more teeth. The mandible can bear a variety of differentiated teeth or other processes. Usually the teeth consist of either molars, usually nonterminal, basally located projections characterized by blunt or flat cusps used primarily for grinding food; or incisors, characterized by more terminally-located prongs with acute to acuminate tips and used for tearing or even piercing food. Insects possess mandibles that can consist entirely of molars, entirely of incisors, some combination of molars and incisors, or even be edentulous. In addition, mandibles may bear basal setae, hairs, denticle ridges or pectines and articulatory processes known as prosthecae or lacinae mobili. Mandibular dentition, articulatory processes and surface vestiture are often cited as evidence for the feeding habits of insects (Isely 1944; Gangwere 1960, 1965; Chapman 1965; Liebermann 1968; Patterson 1984).

4.4.3. **Hypopharnx**

The hypopharynx is an unpaired, single- or multielement extension of the ventral head region. Although the anatomical limits of the hypopharynx are less circumscribed than the gnathal appendages, two recurring features are prominent in many insect groups. These are the medial lingua, or tongue, and the paired, lateral superlingulae--also variously known as the paragnatha, paraglossae or maxillulae (Crampton 1921, Evans 1921), which occur separately or conjointly. The lingua is best interpreted as a multifunctional organ. It is involved in extra-oral digestion since the salivary duct discharges secretions into the oral cavity at the lingual base in many groups. It is also a tonguelike gustatory organ that emplaces food into the true mouth (Smith 1985). In certain adult dipterans, the hypopharynx is modified into a stylet that is furnished with retrally-directed barbs and a terminal salivary duct for injecting proteolytic enzymes into prey.

4.4.4. Maxillae

Maxillae are paired, multielement appendages anchored to the pleural region of the head by a single condylic articulation and several muscular attachments, and are located between the mandibles and labium. The basal or dorsal region of the maxilla consists of two sclerites--a proximal cardo and a more distal stipes, the junction of which is characterized usually by a membranous joint capable of flexion. Muscles responsible for movement of the entire structure or only the cardo have their origin either on the internal head capsule wall or on derivative apodemes in apterygotes (Hoffmann 1905). Alternatively, in pterygotes, such muscles originate from both the head wall and various branches of the endoskeleton, or tentorium (Hudson 1945).

Ventrally, the maxilla consists of two mesially-directed lobes and a distal, segmented palp. The two projecting lobes consist of an inner lacinia and an outer galea. Usually, the lacinia is more sclerotized than the galea and it often bears hairs, brushes or pectinate structures proximally and dentate spines distally. The galea is generally spatulate or otherwise lobelike in form and, like the lacinia, it is capable of some flexion from muscles having their origin in the stipes. The palpus, borne on an often inconspicuous prominence of the stipes, the palpifer, generally comprises five segments that are collectively musculated for rotation, levation and depression, and are individually musculated for flexion (Matsuda 1965). Palps serve primarily as organs of tactile sensation, albeit they can detect gustatory and chemical signals (Chapman 1982).

4.4.5. **Labium**

The labium is an unpaired, multielement appendage informally known as the "lower lip" (Lucas 1923-24) and represents ancestrally the conjoined second maxillae in forms such as the Crustacea (Snodgrass 1935). (As such, it represents a once paired structure that has become unpaired through fusion.) The labium consists of appendiculate and body elements homologous to similar structures occurring in the maxillae. These include ventrally projecting, mesial lobes--a pair of inner glossae and outer paraglossae--and distally a pair of usually three-segmented palpi that are borne on palpigers. The variously sclerotized body of the labium is usually divided into a proximal postmentum and a distal prementum that bears glossae, paraglossae and palpi. The postmentum, in turn, is further subdivided into a proximal submentum and a distal mentum. The postmentum is transversely attached to the neck membrane between the posterior tentorial pits and embryologically represents the fusion of the second maxillary cardines and the ventral labial sclerite. The prementum is divided into a central body of the prelabium, and all appendages and lobes of the postlabium. The prementum is also variously sclerotized and is homologous to the conjoined maxillary stipites; it contains origins of muscles responsible for palp and lobe movement. It is more movable than the postmentum since it contains insertions of retractor and adductor muscles originating from the posterior tentorium.

The glossae and paraglossae, collectively termed the ligula (Chapman 1982), are frequently fused into various central body, lobe and appendage configurations. In some aquatic forms, glossae and paraglossae are fused to form a labial scoop and in dragonfly naiads the entire labium is modified into an elongate, retractile structure with raptorial claws, known as a labial mask (Butler 1904, Lucas 1923-24). In bees only the glossae are conjoined and they are prolonged into a long, hairy tongue. Frequently the glossa and paraglossa on one side are fused to form a broad, tongue-like structure. In some holometabolous larvae, the ligular region is indistinguishably fused to the hypopharynx, forming a composite, silk-producing structure, the spinneret.

4.5. Departures from the Generalized Mouthpart Condition

> Probably no group of structures in the animal kingdom exhibits a better example of the adaptive modification of originally similar, serially arranged organs to very different-looking structures and to diverse functions as insect mouthparts (Metcalf 1929, p. 110).

Mouthparts from two or more head segments have contributed to the formation of composite, multielement structures in many structurally-derived insect groups, especially holometabolous adults. Although intersegmental co-optation of elements has taken numerous themes, the most prominent and recurring one is the formation of stylet-bearing mouthparts ensheathed wholly or partially by a haustellum. Mouthparts with piercing stylets are homologous to mandibulate mouthparts (Frost 1959) and are characterized by three major features. First, the stylets originate by a transformation of primitively robust, transversely-biting mandibles musculated by adductor and abductor muscles into derived, stiletto-shaped, piercing structures characterized by protraction and retraction. (Dajoz [1976] has cogently documented a transformation series from mandibulate mouthparts to stylet-bearing mouthparts among related genera in the beetle family Cerylonidae.) Secondly, most piercing mouthparts are typified by a multielement tubular structure, the haustellum, which is constructed from the labrum and main body of the labium and houses the stylets. Lastly, piercing mouthparts are almost always associated with a sucking pump, either clypeally located or occurring within the pharyngeal region. Stylet-bearing mouthparts are almost always hypognathous or opistognathous and the movable mouthpart ensemble is usually retractable. In some instances stylet-bearing mouthparts occur without a haustellum and thus operate without any channel, guide, or tube for stylet entrainment. Stylet-bearing mouthparts are invariably used for the uptake of liquid food.

Other major deviations from the generalized condition include derived mouthpart types used for feeding on surface fluids. These include forms bearing (i) a siphon, such as butterflies, (ii) a long, hairy tongue, such as bees and (iii) a fleshy expansion of the distal region of the labium, which occurs in "nonbiting" flies. Siphon-bearing mouthparts capitalize on a fusion and elongation of the maxillary galeae into a tubular structure used for inbibing fluids. The presence of a powerful clypeal pump provides sufficient negative pressure to effect flow of fluids into the galeal siphon. Other forms feature a prolongation of the conjoined glossae into a long, flexible tongue used for lapping nectar or similar fluids. As the glossal tongue is withdrawn toward the head, clasping galeae squeeze fluid into the mouth cavity (Harder 1982). An alternative hypothesis holds that a tube is temporarily constructed during feeding by overlapping galeae that form the dorsal and lateral tube walls, and by appressed labial palps that form the ventral tube wall (Snodgrass 1942, 1956). Accordingly, fluid food ascends the glossa by capillary action and is actively sucked into the mouth by action of a cibarial and pharyngeal pump once it reaches the tube. The last major type of modification are forms with a distal, broad, fleshy expansion of the labium, the labellum. Labellum-bearing mouthparts consist of an intricate, microtracheal system used for capillary uptake of surface fluid on the labellum, followed by a labial gutter or similar channel for transportation of the labellar fluid up the proximal part of the labial proboscis and into the mouth.

A unique modification of generalized mandibulate mouthparts occurs in nominally mandibulate larvae of the Planipennia whereby a gracile, falcate mandibulo-maxillary complex is used to suck fluids from prey. This multielement system is dominated by a joining of the mandible and maxillary lacinia to form temporary canals used for secretion of proteolytic enzymes and sucking of liquified prey contents (see Wundt 1961 or Zwick 1967 for detailed discussions). A similar structure occurs among some coleopterous and dipterous larvae, wherein tubular mandibles are used solely to pierce prey and suck prey fluids.

Many other examples of composite mouthpart structures exist, but they are mostly restricted taxonomically to particular families or even genera. For a documentation of the basic groundplan of the insect head and mouthparts and its major departures in fluid-feeding and other groups, see Chaudonneret (1982-1989).

CHAPTER 5

THE VARIABLES: THE USE OF HEAD AND MOUTHPART FEATURES AS FUNCTIONAL INDICATORS

The data-set consists of a matrix of 49 characters, or variables, and 1365 samples, or cases. Each character is subdivided into qualitatively-based character-states, ranging in number from three (Character 5) to nineteen (Character 39). The characters are grouped into three anatomic regions: (i) mouthpart-related features of the head and sense organs (Character-Groups I and II, Characters 1 to 11), (ii) general features of mouthpart structures (Character-Group III, Characters 12 to 17) and (iii) general and specific aspects of particular mouthpart regions (Character-Groups IV to IX, Characters 19 to 49). (A list of character-groups, characters and character-states is provided in Appendix A.)

5.1. Rationalization for Choice of Characters

Several considerations have guided my choice of charac ters and their subdivision into character-states. First, I chose characters present in virtually all hexapods. Second, I have opted for gross characters that are sufficiently coarse-grained that they can yield an appropriate morphologic description of a group as structurally, functionally and ecologically diverse as hexapods, but yet sufficiently fine-grained to provide discrimination among significantly different hexapod subgroups. This delicate balance is expressed by a rejection of those characters that reasonably would be unable to distinguish major mouthpart groups and by acceptance of those gross characters that are a direct expression of general mouthpart function. For example Winston (1979), in an excellent analysis of the maxillolabial complex of apoid bees, provides an example of characters that are too fine-grained to be applicable in this study. Most of Winston's characters, such as presence of a stipital comb, paraglossa/glossa relative length and palpiger vestiture, to mention a few, would not yield sufficient resolving power for the present study. Also, structures such as sensillae (e.g. Baker and Chan 1987) are poorly documented in most primary mouthpart references and are unimportant for determining gross structure. Additionally, I have generally excluded muscle-related characters since their determination is often incomplete, their documentation is exceedingly uneven across most mouthpart studies, and there are numerous problems with "homologization" of muscle-type nomenclature (Matsuda 1965, Smith 1985). Moreover, muscle-related features are rarely preserved in fossils (*vide infra*).

Most important of all, I was particularly concerned in using characters which have direct or indirect functional correlations to various aspects of insect feeding or diet. In this context I have documented anecdotal observations, biometrical studies and functional morphological correlates between the mouthpart characters used in this study and respective diet (Sections 5.3 to 5.11). Thus the principal basis of my choice of characters is that they have strong associations with diet. In this context the most preferable association is direct functional correlation--a functional relationship between a structure and either a feeding-related activity or diet of a hexapod. An indirect functional correlation is a functional relationship between a structure and another, usually adjacent, structure which, in turn, posesses a connection to a particular feeding activity or diet.

There are also more prosaic reasons for my choice of characters. I selected characters that have a high probability of being described in a vast body of mouthpart literature which has considerable variation in intensity and completeness of coverage. (In effect, this means incorporation of all obvious, major, external structures of the insect head and mouthparts.) Also, a decision was also made to select those attributes that would have a high likelihood of being present in specified, well-preserved fossil deposits--the subject of a future study. Thus many typically nonpreservable, internal cranial and mouthpart characters were not used. I also have established the upper limit of variable number at around 50, opting for greater sample coverage instead.

Although hexapod mouthparts exhibit a wealth of structural diversity, I opted to select those characters that, once fulfilling the criterion of dietary or feeding mode relevancy above, represent an eclectic sample of all mouthpart regions (clypeal-labral, "pharyngeal," mandibular, maxillary, labial) and a representative sample of head measures that are appropriate to diet or feeding style. I used several types of characters to express head and mouthpart structure, specifically quality, shape, aspect-ratio (a measure of size), number and an evaluation of mouthpart element co-optation between or among mouthpart regions (Fig. 1). These types of characters logically express a meaningful description of mouthpart form by reference to several and not

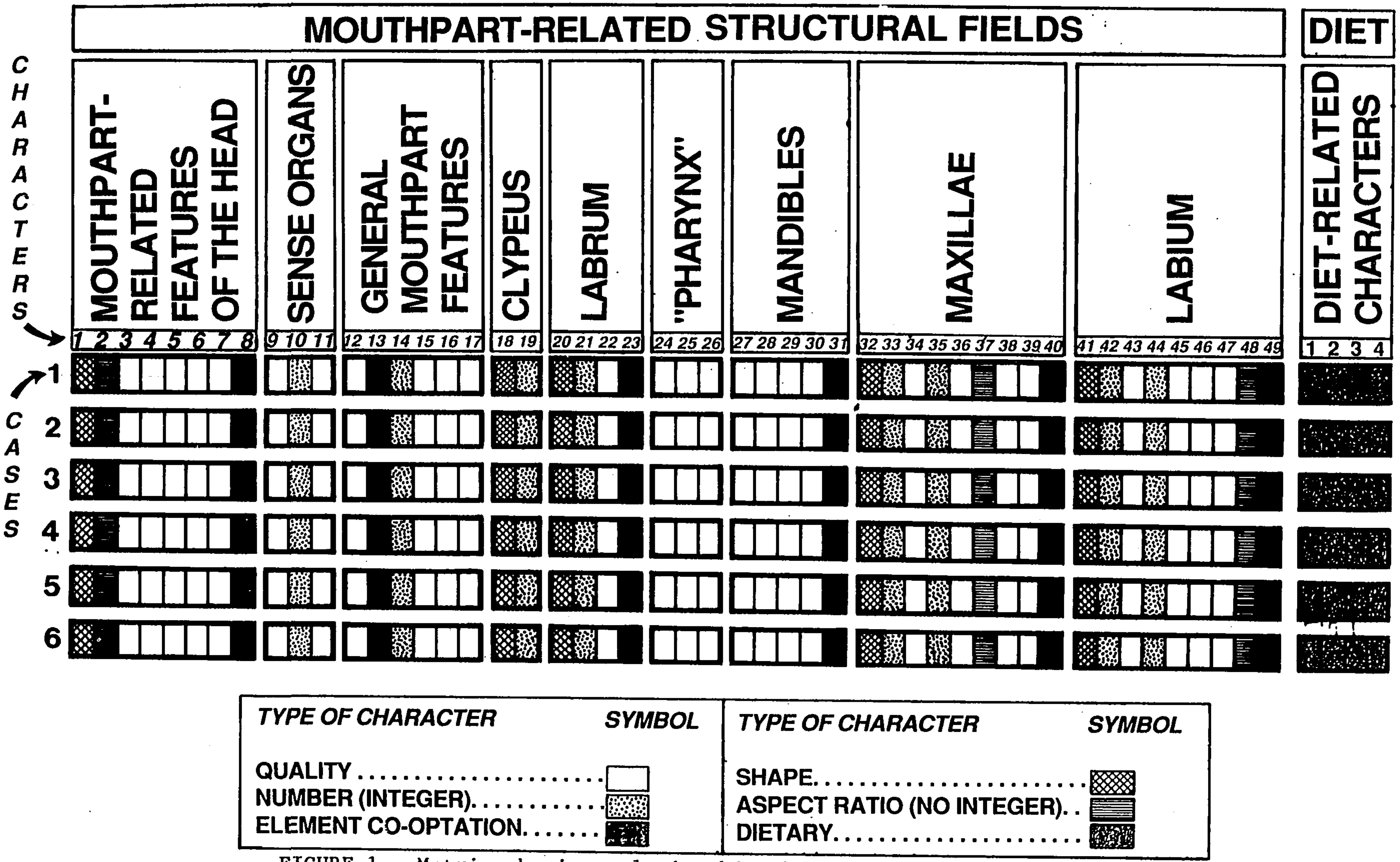


FIGURE 1. Matrix showing relationships between character-groups, groups, characters, and type of characters for cases of the data-set.

only one or two indices of comparison. Although other characters could have been chosen, the ones of the present study succinctly encompass those aspects of gross mouthpart structure (e.g. head shape, mandible type, palpal segmentation) that is likely to interact directly with consumed food materials or participate in a particular feeding mode. It is doubtful whether significantly different results would be obtained if other characters were used that represent different features of the same basic types mentioned above.

Character-states were assigned to each character in the following way. Each character was describable by quality, shape, number, aspect ratio or co-optation with other mouthpart elements (Fig. 1). For each character, character-states were determined initially by a comprehensive survey of the mouthpart literature. These character-states were then used as a tentative, a priori classification system during the formal data-gathering process and were modified on occasion as previously unrealized character-states were encountered. After the data-gathering stage was completed, the character-states for each character were evaluated *a posteriori* for discreteness. On occasion character-states were split into separarate character-states, or character-states were consolidated. Thus the resulting character-state classification represents a three phase process of initial evaluation, ongoing reassessment during gathering of data, and re-evaluation during a final analysis of discreteness. In those cases where it was difficult to split or lump character-states, I opted for a consistency criterion with respect to other character-states of the same character. Thus the degree of difference in the character-state under consideration had to match or exceed the degree of difference among other recognized character-states of the same character.

5.2. Functional Significance of the Characters Used

The characters are arranged hierarchically (Appendix A) and describe various general and specific properties of mouthparts and relevant head features. Both broad-scale (Groups I to IV) and more narrowly-focused (Groups V to IX) characters were used, to ascertain overall mouthpart structure of insects (Fig. 1). Character-groups pertaining to particular mouthpart regions included character-states describing individual elements as well as character-states describing multielement complexes formed by the intimate co-optation of elements within or among mouthpart regions. Examples of single elements include galeal modifications (Character 38) or paraglossal modifications (Character 47), and examples of multielement complexes include basic mouthpart type (Character 12) and participation of the mandibles in a multielement mouthpart structure (Character 31). Notably, correlation exists among those characters that participate in a mouthpart complex occurring within a mouthpart region, or among those characters of various mouthpart regions that contribute elements to the same multielement complex.

The following discussion documents the direct and indirect relationship between a particular character or character-state and some feature of feeding or diet. For purposes of brevity I do not discuss every character-state, nor do I attempt to discuss all major feeding and dietary implications of head or mouthpart structure. Since many of the characters are assemblages of elements that function collectively rather than independently, some of the ensuing discussion necessarily will be repetitive because of separate treatments of the elements in their respective mouthpart region. The functional significance of some characters will undoubtedly be more convincing than others. It is significant that those characters with greater completeness of documentation and cogency of functional interpretation are single elements. Well-documented single elements are the gular region (Character 4), placement of mouthparts on the head capsule (12), mouthpart symmetry (15), hypopharynx type (25), epipharynx type (26), mandible type (28), mandibular dentition (29), galeal modifications (38) and lacinial modifications (39). Multielement exceptions are basic mouthpart type (12) and labial participation in multielement mouthpart structure (49). Furthermore, this discussion is applicable only to the patterns gleaned from the 1365 taxa studied, presumably a representative sampling of insects.

5.3. Character Group I: Head Shape and General Mouthpart-Related Structures

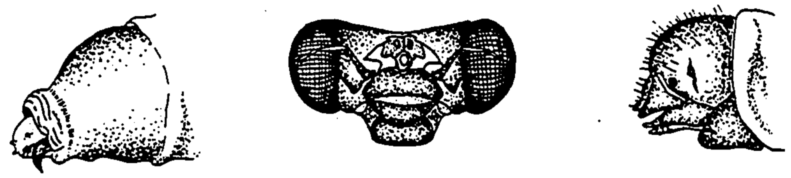
Four of the characters in this character-group (1, 2, 7 and 8) mostly describe general features of the head and proboscis that are related to life-habits and feeding strategy. For example, proboscis-bearing forms generally are fluid-feeders with mouthpart structures designed to reach deep into prey or into plant organs inacessible to forms with more typical mandibulate mouthparts. The other characters (3, 4, 5 and 6) refer to particular head regions or sclerites that are present or developed in conjunction with certain mouthpart states. The association of strong gular development with forwardly-directed mouthparts is a case in point.

5.3.1. Head Shape (Character 1)

Most insects bear a head that is approximately spheroidal in shape (Fig. 2). However, highly visual adult forms that rely primarily on sight for location of food have well-developed, laterally placed eyes and possess transversely-elongated heads (odonatans, myrmeleontid planipennians and lepidopterans, for example). Forms with vertically elongated rostra (nemopterid planipennians, mecopterans) or downwardly-hanging mouthparts (dipterans, most hymenopterans) tend to be fluid-feeders or small-particle feeders (Hobby and Killington 1934, Picker 1987). Forms with anteriorly prolonged heads, as a group, lack any pattern between head shape and feeding or diet, but include forms such as herbivorous orthopteroid insects, sanguinivorous heteropterans and seminivorous curculionoids. Many holometabolous larvae are a special case: they are specialized folivores with a head capsule that is partly retracted into the thorax.

There is limited evidence suggesting that head mass and size can be a direct consequence of diet type. Orthopterans chewing on tough grass possess twice the head mass than conspecific forms feeding on soft forbs (Bernays 1986, Bernays and Hamai 1987). Similarly, head size is markedly larger in soldier castes than in other castes of the same species (Wheeler 1927). In these and other instances, increases in head mass and size correlate with jaw development and hence greater

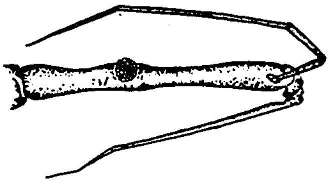
HEAD SHAPE



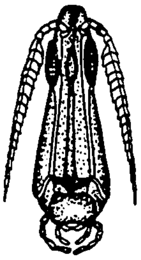
A. INCONSPICUOUS.
DIP: *Tritoxa incurva* Loew.
Larva, [Allen & Foote 1975].

B. TRANSVERSE.
ODO: *Lestes barbatus* (Fabricius).
Adult, [Strenger 1952].

C. QUADRATE.
COL: *Hylecoetus lugubris* Say.
Larva, [Peterson 1951].



D. PORRECT.
HET: *Hydrometra stagnorum*
Linneaus. Adult, [Cobben 1978].



E. VERTICAL.
ORT: *Tryxalis nasuta* Fischer.
Adult, [Strenger 1942].

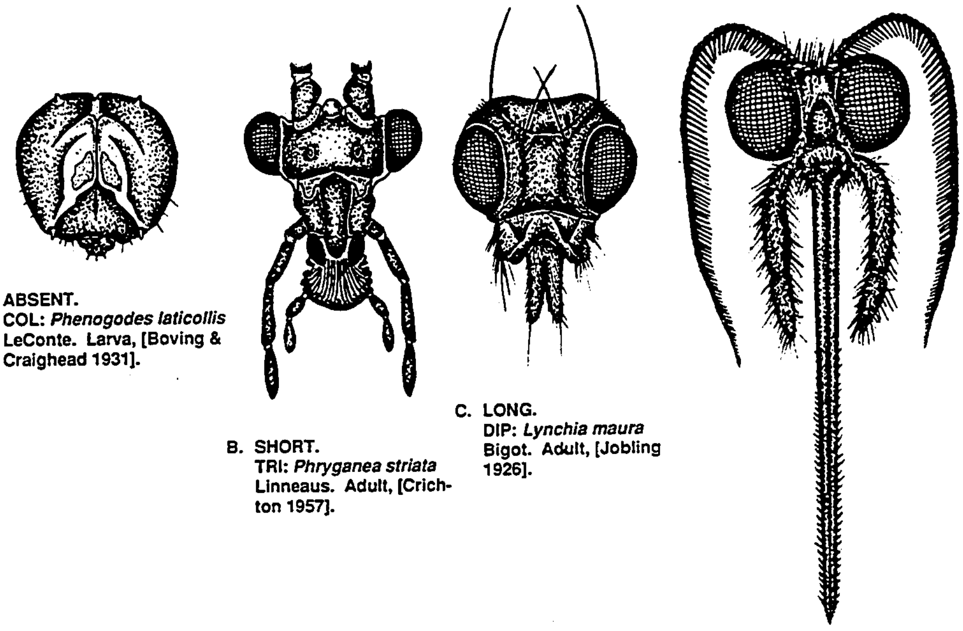
FIGURE 2. Character-states of Character 1: head shape. Not drawn to scale.

mandibular muscle mass (Metcalf et al. 1962). Since mandibular muscle mass is distributed unevenly in the head capsule, associated changes in head shape should be expected. For particle-feeders in dipteran larvae, changes in head capsule length/width ratios are associated with specific feeding styles (Dahl et al. 1988).

5.3.2. Rostrum or Proboscis Development (Character 2)

A rostrum, consisting of an anterior prolongation of the head capsule with mouthparts situated terminally, and a proboscis, characterized by elongate mouthparts projecting significantly beyond the head capsule, are both indicators of feeding behaviors typified by the probing or thrusting of the food-reaching organs deep into unexposed tissue. In rostrum-bearing forms such as weevils and other floricolous beetles, terminally-located mandibulate mouthparts process the deeper nonfluid tissues of plants (Crowson 1981) before pharyngeal uptake, whereas proboscate forms such as herbivorous bugs generally are fluid-feeders that possess a sucking pump for direct imbibation of (sometimes extraorally digested) fluid food (see Fig. 3 for examples).

For pollenivorous hoverflies (Diptera), Gilbert (1988, oral presentation) presented data indicating a strong association between shape and length of a proboscis and diet type. Among nectarivorous lepidopterans, there is a strong association between proboscis length and depth of the nectar-bearing floral tube (Emmel 1971, Barth 1985, Nilsson et al. 1987). Naumann (1937) and Gohrbandt (1940) have demonstrated strong correlations between decreased proboscis length and wing



ROSTRUM OR PROBOSCIS

A. **ABSENT.**
COL: *Phenogodes laticollis* LeConte. Larva, [Boving & Craighead 1931].

B. **SHORT.**
TRI: *Phryganea striata* Linneaus. Adult, [Crichton 1957].

C. **LONG.**
DIP: *Lynchia maura* Bigot. Adult, [Jobling 1926].

D. **VERY LONG.**
LEP: *Calpe thalictri* Burkhardt. Adult, [Banziger 1970].

FIGURE 3. Character-states of Character 2: rostrum or proboscis. Not drawn to scale.

reduction (an expression of environmental mobility and perhaps diet) in many butterfly species. The same relationship was found by Harder (1981) for bumblebees.

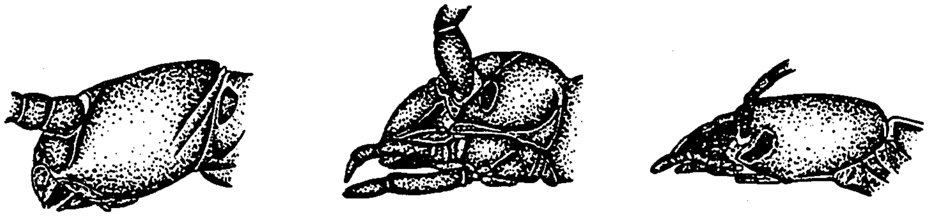
5.3.3. Genal Region or Malar Space (Character 3)

The genal region is, in part, the lateral head capsule wall, and its development corresponds to the degree of separation of the sensory organs (antennae, ocelli and especially compound eyes) from the organs of feeding (Denis and Bitsch 1973) (Fig. 4). The gena usually encompasses the compound eyes toward the vertex of the head capsule and inferiorly borders the pleurostoma, a thin, narrow membrane or sclerite that bears the mandibular articulations (DuPorte 1957). The gena is best developed in hypognathous forms (Snodgrass 1935) with vertically prolonged heads. In hemipteroid forms, the "genal region" is occupied by the maxillary plate (Bourgoin 1986a), a sclerite separating the base of the labial haustellum from the generally well-developed eyes. Special cases of genal development occur in larvae. In many lepidopteran larvae the gena envelops the ocelli and much of the dorsal cranial capsule; among cyclorrhaphan larvae the gena participates in formation of the cephalopharyngeal capsule--a structure surrounded by tissue originating from the thorax (Teskey 1981c).

5.3.4. Gular or Hypostomal Region (Character 4)

The gula or hypostomal region represents the separation of the occipital region--namely the foramen magnum--from the posteriormost

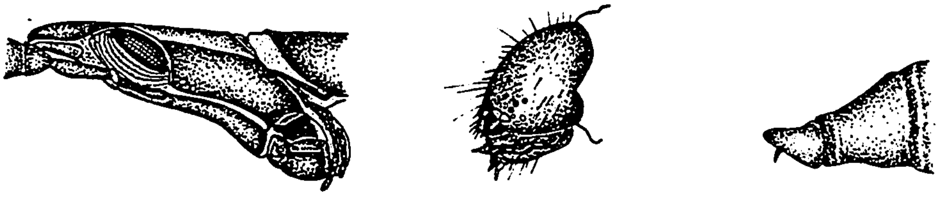
GENAL REGION OR MALAR SPACE



A. **GENA ABSENT.**
DPL: *Campodea chardardi* (Conde). Adult, [Francois 1970].

B. **GENA PROMINENT.**
DER: *Arixenia jacobsonii* Burr. Adult, [Giles 1963].

C. **MODERATELY TO MINIMALLY DEVELOPED.**
EMB: *Embia ramburi* Rimsky-Korsakov. Adult, [Rahle 1970].



D. **GENA EXPANSIVE.**
ORT: *Keyacris scurra* (Rehn). Adult, [Blackith & Blackith 1966].

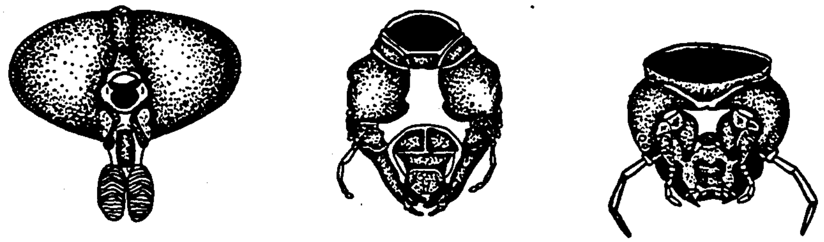
E. **COMPRISING MOST OF THE CRANIUM.**
LEP: *Depressaria heracliana* (De Geer). Larva, [Peterson 1948].

F. **PART OF CEPHALOPHARYNGEAL SKELETON.**
DIP: *Calliphora vomitoria* Linneaus. Larva, [Roberts 1971].

FIGURE 4. Character-states of Character 3: genal region or malar space. Not drawn to scale.

extension of the mouthparts (Fig. 5). Usually the gula is a posterior extension of the labial submentum, the demarcation of which is often absent or vague. A well-developed gula is an expansive, ventral plate (Jeannel 1960) surrounded laterally by the genal or postgenal region. Alternatively, it may be a faint, linear trace representing the near-complete medial convergence of the postgenae and oftentimes is designated as the "gular suture" (Snodgrass 1935, but see Hinton 1963). A poorly developed gula is an abbreviated, narrow band transversely straddling the cervical membrane, or foramen magnum, and the submentum (Snodgrass 1935). A well-developed gula is identified with the prognathous condition, characterized by anterior, forwardly-directed mouthparts (Walker 1931a, DuPorte 1962, Hinton 1963, Matsuda 1965), whereas the gula is often narrow or even absent in forms with downwardly or backwardly directed mouthparts (DuPorte 1962). In some holometabolous adults (Diptera, Hymenoptera), the region of separation of the mouthparts from the foramen magnum is known as the hypostomal or postgenal bridge, or the malar space, and it represents the medial fusion of the posterioventral region of the head capsule (Snodgrass 1935, Chapman 1982). An analogous region, the postgenae, occurs in many holometabolous larvae (Anderson 1936). Because of these nomenclatural differences, I have assessed the character as the degree of separation of the anteriormost identifiable labial sclerite from the foramen magnum or cervical membrane, irrespective of the name of the intervening structure.

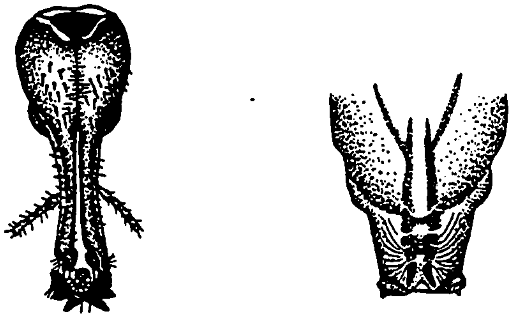
GULA OR HYPOSTOME



A. ABSENT OR INCONSPICUOUS.
DIP: *Tabanus sulcifrons* Macquart.
Adult, [Bonhag 1951].

B. PROMINENT.
MEG: *Corydalus* sp. Larva,
[Snodgrass 1935].

C. MODERATELY TO MINIMALLY DEVELOPED.
COL: *Silpha*, sp.
Larva, [Snodgrass 1935].



D. PROLONGED, WITH PREGENA & POSTGENA.
COL: *Rhynchites auratus* Scopoli.
Adult, [Brack-Egg 1973].

E. PART OF CEPHALOPHARYNGEAL CAPSULE.
DIP: *Phormia regina* (Meigen).
Larva, [Teskey 1981a].

FIGURE 5. Character-states of Character 4: gula or hypostome. Not drawn to scale.

5.3.5. Lorum, or Mandibular Plate (Character 5)

The lorum of Snodgrass (1935), also known as the mandibular plate (Matsuda 1965), is a sclerite between the food-pump region of the fronto-clypeus and the "genal" area in hemipteroid insects. It appears to be associated with a well-developed clypeal pump and may be involved in supporting and anchoring the basal portion of the labial beak to the head capsule.

5.3.6. Frontal and Vertical Region (Character 6)

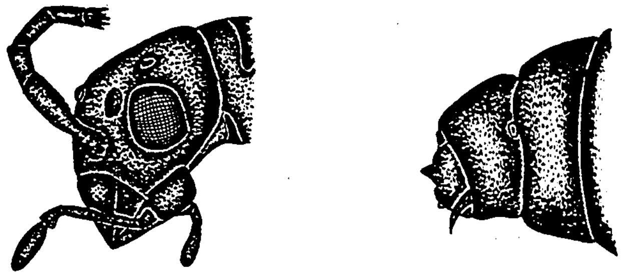
The frontal and vertical region principally comprises the frons and, when the epistomal suture is absent, the proximal portion of the clypeus. The frons is the triangular-shaped, interocular facial area of the cranium, delimited by the epistomal suture distally and the frontal sutures laterally. It bears the median ocellus and origins of the labral muscles (Snodgrass 1935). Special modifications of the generalized condition include intrusion of the clypeus into the frons, as in caterpillars, resulting in a frons with an inverted-Y shape (Snodgrass 1928, but see Forbes [1910] for an alternative homology); prolongation of the frontal region anteriorly in bugs; participation of the frons in the formation of the cephalopharyngeal skeleton in muscomorph fly larvae (Ludwig 1949); and formation of a lunate, ptilinial fissure on the frons of adult schizophoran flies (McAlpine 1981). Although less demonstrable than the analogous condition of gular development, the anterior extension of the frontal region appears as an indicator of the degree to which the head capsule has become prolonged for accomodation of terminal, prognathous mouthparts. Lepidopteran larvae display an opposite trend, whereby the clypeofrontal region of the head capsule has been sunk into the upper head capsule for reception of hypognathous, proximally-situated mouthparts.

5.3.7. Head Protractability/ Retractability (Character 7)

The ability to retract the head capsule into the anterior region of the thoracic cavity is a trait found in many holometabolous larvae, notably maggots (Teskey 1981e) and caterpillars (Fig. 6). Head retraction requires the presence of powerful muscles originating in the thorax (Schremmer 1956) and their insertion on either endoskeletal head structures or exoskeletal apophyses (Randriamamonjy 1963). Such a feature may be advantageous in the manipulation or leverage of leaf material by the mandibles of caterpillars or the protraction of mouthhooks into prey items by certain maggots. The evidence for this, however, is not strong.

5.3.8. Head-Associated Feeding Modifications (Character 8)

Many insects have structures for detecting, acquiring or processing food that do not involve typical structures of modifications of the head or mouthparts. Most of these structures involve modification of the prothorax or its appendages. Prothoracic participation in head structure is shown by the "fusion" of the head capsule with the thorax in strepsipterans, resulting in formation of a cephalothorax (Pierce 1918, Bohart 1962). A food-processing structure typically located in the



A. NONPROTRACTILE.
ZOR: *Zorotypus hubbardi* Caudell.
Adult, [Crampton 1920].

B. PROTRACTILE.
DIP: *Sciadocera rufomaculata*
White. Larva, [Fuller 1934].

FIGURE 6. Character-states of Character 7: Head protractability/ retractability. Not drawn to scale.

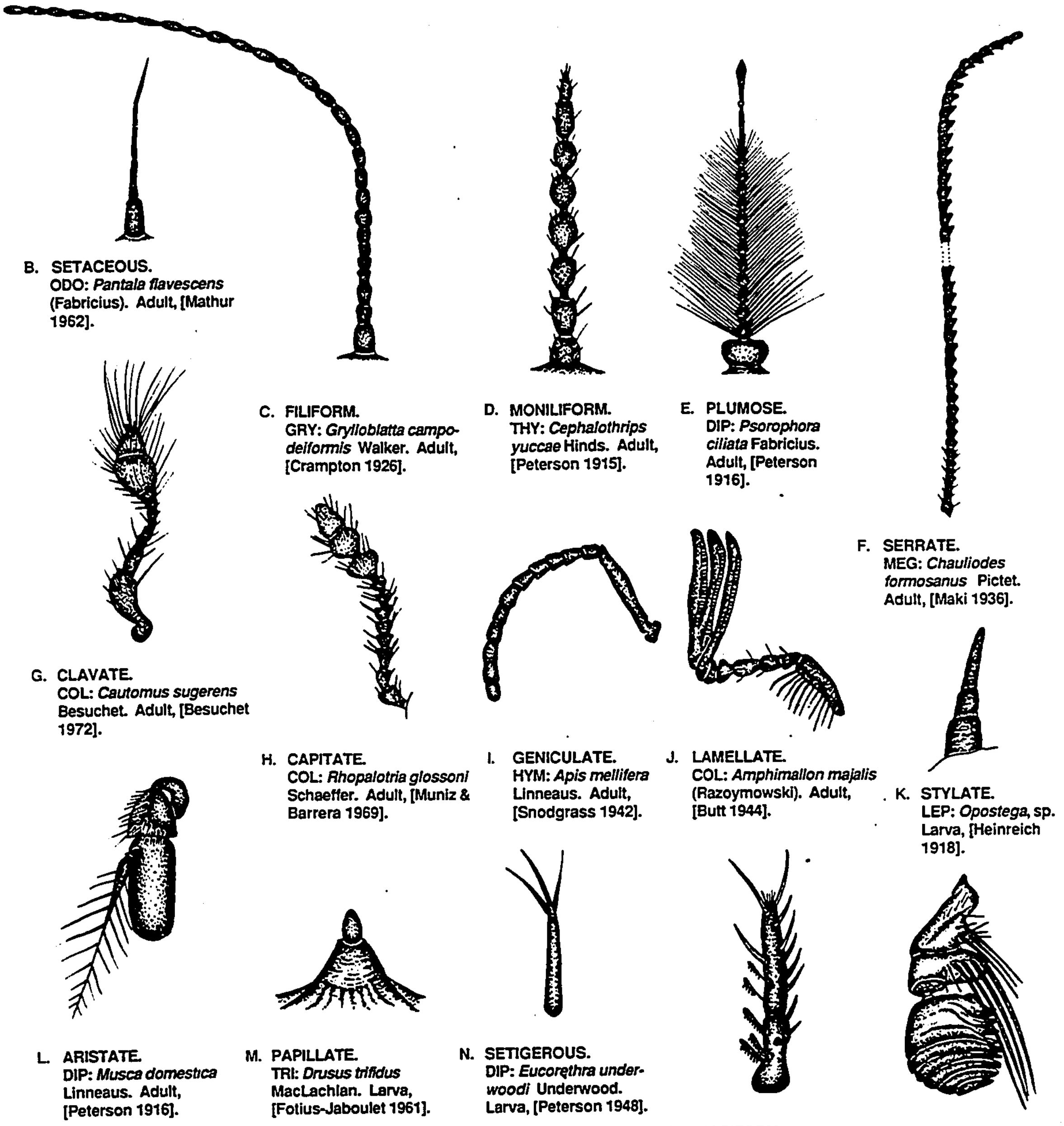
thorax is the particle-filtering apparati located in the esophagi of aquatic dipteran larvae (Hennig 1935; Schremmer 1949, 1951). Prothoracic legs are occasionally used in the feeding system--notably the raptorial legs of adult dragonflies, mantids and waterscorpions (Asahina 1954, Levereault 1936, Hamilton 1931, respectively) and the antennalike, sensory prothoracic legs of the telsontails (Gillott 1980). Posteriorly-directed spines in fleas (e.g. the genal comb) assist as an anchor for the insect to the substrate during feeding (Wenk 1953). Lastly, forcipate cerci are used as accessory sets of "mandibles" in japygid entotrophs (Wootton 1984) and earwigs (Popham 1959) for prey capture or defense.

5.4. Character-Group II: Sense Organs of the Head

Since insects must sense and locate food before it is dispatched and brought to the mouthparts, it is important that food-locating sense organs be included in this study. Notable in this regard are antennae, eyes of several types, and palps. The first two are included here; palps are considered under their respective mouthpart regions. Various other sensory structures, such as leg taste receptors, are not included.

5.4.1. Antennae (Character 9)

Antennae are extremely varied in form (Fig. 7)--a condition that probably mirrors function (Wootton 1984). Whereas antennae in many poorly-sighted groups are used for tactile communication (Corbière 1967), in most groups antennae are the primary or secondary sensors for detecting olfactory, gustatory, chemoreceptive, mechanoreceptive and



B. SETACEOUS.
ODO: *Pantala flavescens* (Fabricius). Adult, [Mathur 1962].

C. FILIFORM.
GRY: *Grylloblatta campodeiformis* Walker. Adult, [Crampton 1926].

D. MONILIFORM.
THY: *Cephalothrips yuccae* Hinds. Adult, [Peterson 1915].

E. PLUMOSE.
DIP: *Psorophora ciliata* Fabricius. Adult, [Peterson 1916].

F. SERRATE.
MEG: *Chauliodes formosanus* Pictet. Adult, [Maki 1936].

G. CLAVATE.
COL: *Cautomus sugerens* Besuchet. Adult, [Besuchet 1972].

H. CAPITATE.
COL: *Rhopalotria glossoni* Schaeffer. Adult, [Muniz & Barrera 1969].

I. GENICULATE.
HYM: *Apis mellifera* Linneaus. Adult, [Snodgrass 1942].

J. LAMELLATE.
COL: *Amphimallon majalis* (Razoymowski). Adult, [Butt 1944].

K. STYLATE.
LEP: *Opostega*, sp. Larva, [Heinreich 1918].

L. ARISTATE.
DIP: *Musca domestica* Linneaus. Adult, [Peterson 1916].

M. PAPILLATE.
TRI: *Drusus trifidus* MacLachlan. Larva, [Fotius-Jaboulet 1961].

N. SETIGEROUS.
DIP: *Eucorethra underwoodi* Underwood. Larva, [Peterson 1948].

O. PALPIFORM.
PLA: *Aleuropteryx loewi* Klapalek. Larva, [Rousset 1966].

P. SPATHULATE.
SIP: *Ctenocephalus canis* (Curtis). Adult, [Wenk 1953].

FIGURE 7. Character-states of Character 9: antennae. Not drawn to scale.

even auditory signals from host plants or animals (Plateau 1885, Glaser 1927, Snodgrass 1960, Schneider 1964, Baker and Chan 1987). Long antennae, such as filamentous, setaceous or moniliform types, are probably used tactilely (Schneider 1964, Chapman 1982). Crowson (1981) has cited filiform antennae as a recurring, adaptive character among floricolous beetles. In a taxonomically broad study of adult dipterans, Smith (1919) concluded that dipterans possess organs sensitive to touch, taste and smell, although there was not a definite association between filiform, stylate and aristate antennae and particular life-habits. Many larval beetles possess palpiform antennae used in manipulation of prey items during mastication (Pavlovsky 1922). Other holometabolous larvae have antennae richly supplied with several types of mechanoreceptive and chemosensory sensillae (Baker and Chan 1987), or have apparently functionless nubbins as antennae or completely lack antennae (Richards and Davies 1977). (See Staedler [1977] for a summary of antennal sensory mechanisms.)

5.4.2. Ocelli, Pseudocelli and Stemmata (Character 10)

Ocelli, pseudocelli and stemmata are light-sensitive organs (Richards and Davies 1977, Chapman 1982). There is a broad range of light sensitivity in these organs, ranging from some ocelli, which are minimally involved in distinguishing light-intensity levels, to stemmata of certain lepidopteran larvae, which resolve and differentiate color (Ishikawa 1969). The presence of ocelli in some species is strongly positively correlated with wing development and hence flight (Kalmus

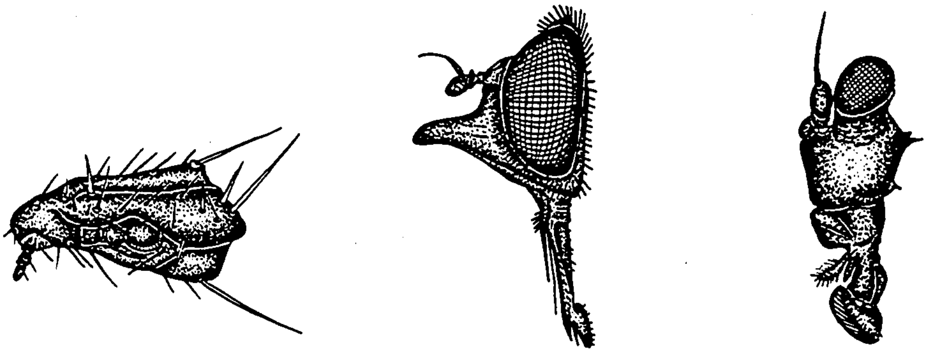
1945, Goodman 1970). For a few forms, there is also strong evidence indicating that under decreased light levels, ocelli operate synergistically with the compound eyes to stimulate a positive photokinetic response whereas at increased light levels the response is a negative photokinesis (Goodman 1970). There also appears to be a relationship between levels of ocellar illumination and antennal stimulation (Mimura et al. 1969). Larval stemmata, unlike ocelli, are capable of independently producing images and collectively represent the visual field as a coarse mosaic (Dethier 1942, 1943). Pseudocelli are light-sensitive regions in proturans.

All three organs are involved, in various ways, with recognition of light-intensity levels, without the clear direct advantage of highly resolved, discrete image formation found in compound eyes. Thus their presence and development is an indicator, though indirecly, of partial recognition of environmental cues, including the detection and active pursuit of food.

5.4.3. Compound Eyes
(Character 11)

Compound eyes are an obvious component in the repertoire of sensory organs available to an insect for detection of food (Fig. 8). While virtually all pterygote compound eyes are homologous (Paulus 1974), there is amazing functional divergence among various species--honeybees perceive color (Menzel 1975) while others, such as grasshoppers, are capable of motion detection (Kaiser 1975, Kien 1975) and a few, including some ants, possess form sensitivity for either spots or object edges

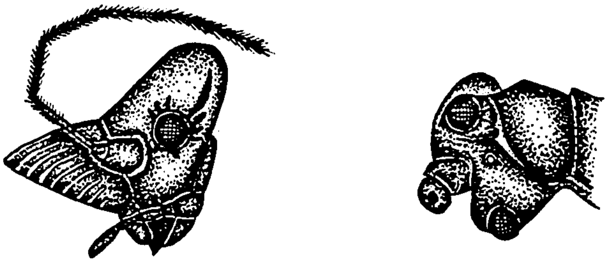
COMPOUND EYES



A. **ABSENT.**
MAL: *Trimenopon jenningsi* Kellogg & Paine. Adult, [Stowe 1943].

B. **PROMINENT.**
DIP: *Rhingia nasica* Say. Adult, [Vockeroth & Thompson 1987].

C. **STALKED.**
DIP: *Sphyracephala brevicornis* Say. Adult, [Peterson 1916].



D. **MODERATELY DEVELOPED.**
PSO: *Rhinopsocus arduus* Badonnel & Lienhard 1988. Adult, [Badonnel & Lienhard 1988].

E. **DIVIDED INTO SEPARATE UNITS.**
HOM: *Aplomorpha pharetrata* (Schraeder). Adult male, [Theron 1968].

FIGURE 8. Character-states of Character 11: compound eyes. Not drawn to scale.

(Northrop 1975, Mazokhin-Porshnyakov 1975). Forms with large, especially well separated eyes (stereoscopy?) have inconspicuous antennae and are largely visual predators with carnivorous diets (Chapman 1982, Wootton 1984). This is especially demonstrable in aerial pursuit of species-specific prey, where visual cues are used for initial contact of prey on the wing. Blind insects or those with rudimentary eyes are often either tactile encounter-predators or are noncarnivorous. A special eye character is a divided eye consisting of separate units, a structure that usually indicates separation of feeding function from other functions (Jeannel 1960), such as predator avoidance and mate recognition.

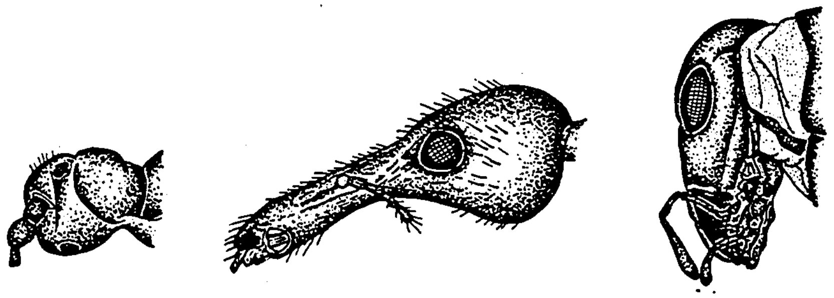
5.5. Character-Group III: General Features of Mouthpart Apparati

Before a characterization of elements from particular mouthpart regions can be done, certain general aspects of the mouthpart complex must be established. Relevant general mouthpart features include the anatomic placement, fundamental type, symmetry and protractability of the mouthpart complex. A related character is the presence of a dilative food pump, which is possessed by virtually all insects, though its number and location can vary. A more restrictive, discrete character, pertaining to stylet-bearing mouthparts, is stylet number.

5.5.1. Mouthpart Placement on the Head Capsule (Character 12)

The relative orientation of the mouthparts on the head capsule is strongly associated with insect feeding habits (Fig. 9). The primitive

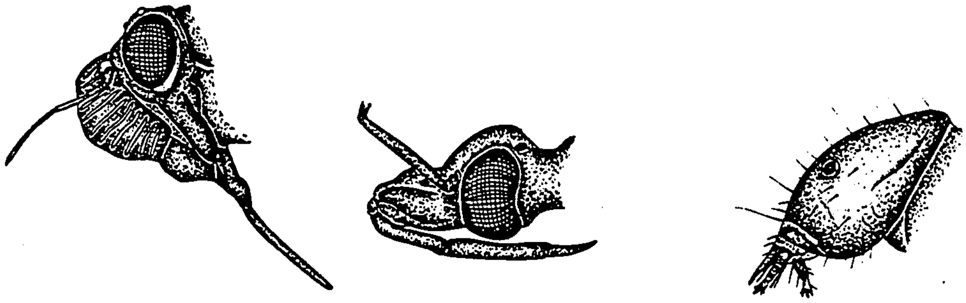
MOUTHPART PLACEMENT ON THE HEAD CAPSULE



A. AGNATHOUS.
HOM: *Lecaniodiaspis elytropappi* Munting & Giliomee. Adult male, [Munting & Giliomee 1967b].

B. PROGNATHOUS.
COL: *Rhynchites auratus* Scopoli. Adult, [Brack-Egg 1973].

C. HYPOGNATHOUS.
ORT: *Amblycorypha oblongifolia* (De Geer). Adult, [Kramer 1944].



D. OPISTOGNATHOUS-AUCHENORRHYNCHOUS.
HOM: *Magicicada septendecim* (Linneaus). Adult, [Snodgrass 1921].

E. OPISTOGNATHOUS-STERNORRHYNCHOUS.
HET: *Triatoma* sp. Adult, [Barth 1953].

F. ENTOGNATHOUS.
PRO: *Acerentomon propinquum* (Conde). Adult, [Francois 1969].

FIGURE 9. Character-states of Character 12: mouthpart placement on the head capsule. Not drawn to scale.

state for pterygote insects is the location of mouthparts under the head capsule, the hypognathous condition (Snodgrass 1960, Hennig 1981: 295, Chapman 1982; but see Walker 1932). Hypognathous mouthparts are found mostly in herbivorous insects, especially those with laterally compressed or cylindrical body forms that feed on foliage (Walker 1932, Snodgrass 1960). Less commonly hypognathism occurs among carnivorous species that are ambush predators and have special adaptations for subduing prey, such as raptorial forelegs (Mantodea) or a labial mask (Odonata larva) (Walker 1932).

The prognathous and opistognathous mouthpart placements are structurally derived. The prognathous condition, characterized by an anterior projection of the mouthparts, is associated with gular expansion (Character 4) and typifies carnivorous species that engage in pursuit predation and dispatch their prey with usually prominent mandibles (Walker 1932). Prognathous mouthparts also occur on soil-burrowing and wood-boring adults (such as weevils) or larvae (such as buprestids) (Walker 1932). The opisthognathous condition characterizes fluid-feeding haustellate forms and consists of two major variations. (1), auchenorrhynchous mouthparts, whereby the sessile beak slopes posteriorly and downward, and appear to originate from the cervical membrane. (2), are stenorrhynchus mouthparts, whereby the beak is capable of being retracted between the legs when not in use (Snodgrass 1960).

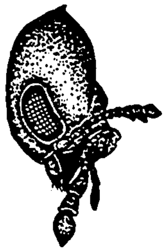
Within hexapods, pterygote entognathy is another derived condition and consists of short, stylet-bearing mouthparts housed in a buccal sac (see Manton 1977). In pterygotes it is present in predominantly fluid-feeding forms (sucking lice, thrips), but among apterygotes it is seemingly a primitive condition associated with feeding on relatively soft, immobile material (McNamara 1924).

5.5.2. Mouthpart Basic Type (Character 13)

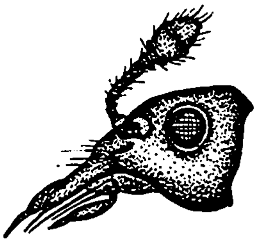
No other data-set character has as much implications for feeding and diet as mouthpart type, however defined (Fig. 10). Although the goal of this study is to ascertain *a posteriori* the fundamental mouthpart *Baupläne* among extant insects, such a salient and crucial character cannot be ignored in the initial analyses of this study. This scheme is based primarily on structural criteria and focuses especially on (i) the presence or absence of functional mouthparts, (ii) mandible shape and deployment, (iii) labium structure and co-optation and (iv) whether the maxillary galeae are conjoined.

These four factors grossly correspond to overall diet. Mouthparts with transversely-biting mandibles ingest solid food whereas protracting-and-retracting stylet-bearing mouthparts are designed to obtain biologically-enclosed, fluid food. Certain larval forms with tubular mandibles or mandible/maxilla complexes are similarly, but secondarily, equiped to pierce and suck out the fluid contents of prey. Siphon-, labellum- and glossa-bearing mouthpart types feed on exposed surface fluids and use principles of active siphoning, capillary adsorption and squeezing, in various combinations, to imbibe food (Barth 1985). Species without functional mouthparts do not feed.

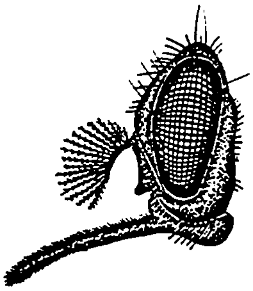
MOUTHPART BASIC TYPE



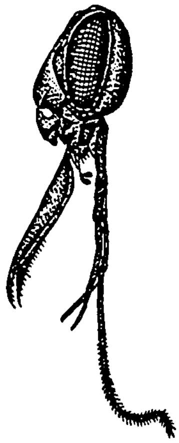
A. MANDIBULATE.
COL: *Epilachna varivestus* Mulsant. Adult, [Butt 1951].



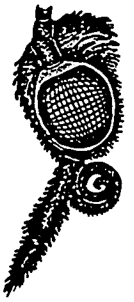
B. STYLATE-NONHAUSTELLATE.
COL: *Cerylon sugerens* Besuchet. Adult, [Besuchet 1972].



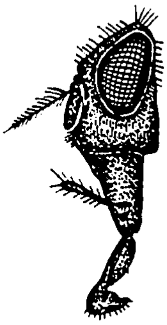
C. STYLATE-HAUSTELLATE.
DIP: *Glossina palpalis* Robineau-Desvoidy. Adult, [Jobling 1933].



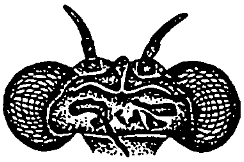
D. GLOSSATE.
HYM: *Anthophora* sp. Adult, [Demoll 1908, Michener 1944].



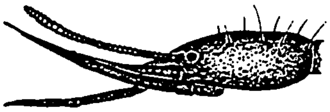
E. SIPHONATE.
LEP: *Elachista madarella* (Clemens). Adult, [Braun 1948].



F. LABELLATE.
DIP: *Calliphora erythrocelphala* Linneaus. Adult, [Graham-Smith 1930].



G. NONTROPHIC.
EPH: *Hexagenia recurvata* Mogan. Adult, [Murphy 1922].



H. MANDIBULO-SUCTORIAL.
PLA: *Neurorthus fallax* (Rambur). Larva, [Zwick 1967].

FIGURE 10. Character-states of Character 13: mouthpart basic type. Not drawn to scale.

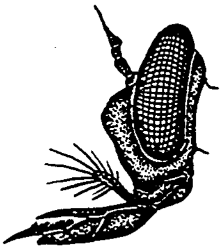
5.5.3. Stylet Number (Character 14)

For stylet-bearing mouthparts ensheathed within a haus tellum, stylet number is often an important descriptor of mouthpart subtype (Fig. 11). Dipteroid and hemipteroid haustellate mouthparts are capable of maximally bearing four and six stylets, respectively, and often there are characteristic stylet numbers that are associated with particular diets or feeding strategies. Most hemipteroid mouthparts are constructed with a pair of stylate mandibles and maxillae that are characterized by interlocking, sliding stylets in pairs that work in co-ordination and apposition, often for deep penetration of plant or animal tissue (Cobben 1978). By contrast, dipteroid forms possess noninterlocking, fasiculate stylets, frequently odd in number, and including a hypopharyngeal stylet for injection of various enzymes, such as proteolytic enzymes for predatory forms (Whitfield 1925) and anticoagulant enzymes for sanguinivorous forms (Jobling 1933). Stylet-bearing mouthparts lacking a haustellum are highly variable in stylet number. Because of occasional departures from the above patterns, many of the above associations are not exact and must be regarded only as generalizations.

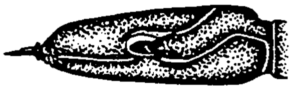
5.5.4. Mouthpart Symmetry (Character 15)

Mouthpart asymmetry takes two basic forms in insects: major asymmetry of the entire mouthpart complex, found only in the Thysanoptera, and relatively minor asymmetries of individual elements, especially mandibles, in various insect groups (Fig. 12). Major mouthpart asymmetry in the Thysanoptera consists of supression of the right

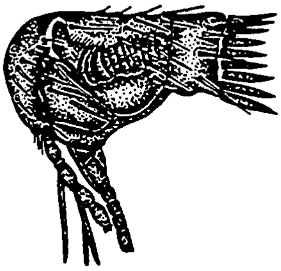
MOUTHPART STYLET NUMBER



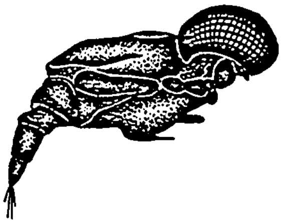
B. **STYLETS ONE.**
DIP: *Proctacanthus* sp.
Adult, [Snodgrass 1943].



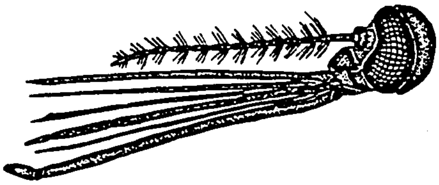
C. **STYLETS TWO.**
ANO: *Haematopinus suis* (Linneaus). Adult, [Stojanovich 1945].



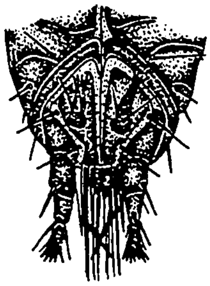
D. **STYLETS THREE.**
SIP: *Cratynius crypticus* Hopkins & Traub. Adult, [Hopkins & Traub 1955].



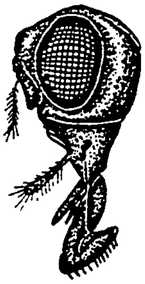
E. **STYLETS FOUR.**
HET: *Gelastocoris oculatus* (Fabricius). Adult, [Parsons 1959].



F. **STYLETS SIX.**
DIP: *Anopheles*, sp.
Adult, [Crampton 1942].



G. **STYLETS NINE.**
PRO: *Acerentomon propinquum* (Conde). Adult, [Francois 1959].



H. **STYLETS GREATER THAN NINE.**
DIP: *Scatophaga furcata* (Say).
Adult, [Peterson 1916].

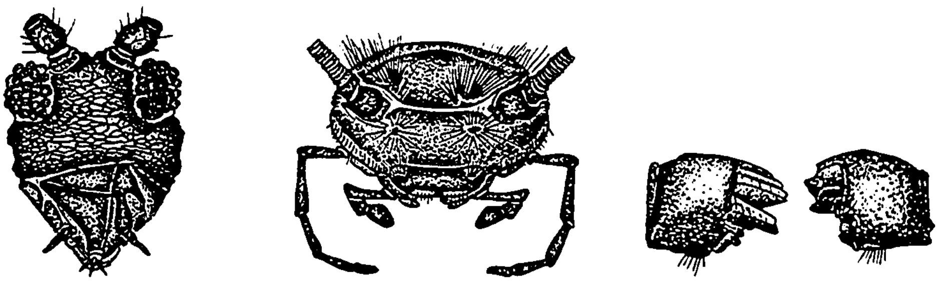
FIGURE 11. Character-states of Character 14: mouthpart stylet number. Not drawn to scale.

mandible and an asymmetrical rearrangement of mouthpart-related sclerites that form the oral cone (Garman 1896, Borden 1915). This has been interpreted as an adaptation for pollen-feeding that occurred in a generalized hemipteroid ancestor (Grinfel'd 1959).

Minor mouthpart asymmetry is rampant among virtually all groups of insects and it is best demonstrated for mandibles in mandibulate insects. The best-documented group in this regard are the Orthoptera, which are frequently characterized by asymmetries of both mandibular size and shape, as well as variation in cusp number, position and size between the right and left mandibles (Ninninger 1915, Isely 1944, Chapman 1964, Gangwere 1965, 1972). This pattern occurs in other groups such as mayfly naiad mandibles (Morgan 1913, Murphy 1922) and adult mandibulate moths (Tillyard 1923, Hannemann 1956). In almost all instances, such mandibular asymmetries have been explained as structures mechanically suited to feeding on specific diet types.

5.5.5. Food Pump
(Character 16)

Food pumps are qualitatively divided into two types: those that are enlargements of the pharyngeal region and those that are expansions of the clypeal or clypeofrontal area. Pharyngeal, or cibarial, pumps are associated with mandibulate forms which ingest solid food; they undergo pharyngeal compression to effect the "vacuuming" of food from the preoral chamber to the oesophagus (Snodgrass 1935, Beutel 1986). When this process is reversed, there is expulsion of salivary gland secretions for extraoral digestion.



MOUTHPART SYMMETRY

A. **MULTIELEMENT ASYMMETRY.**
THY: *Heliothrips femoralis* (Reuter). Adult, [Peterson 1915].

B. **SYMMETRY.**
TYN: *Thermobia domestica* (Packard). Adult, [Chaudonneret 1950].

C. **SINGLE ELEMENT ASYMMETRY.**
ORT: *Xenocheila zarundnyi* Uvarov. Adult, [Chapman 1966].

FIGURE 12. Character-states of Character 15: mouthpart symmetry. Not drawn to scale.

By contrast, clypeal pumps are morphologically distinct structures on the upper face of insects that connect an outer, extensible sclerite to an inner, dorsal, pharyngeal diaphragm by means of powerful dilator muscles (Snodgrass 1947, Backus 1985). (See Smith [1985] for a discussion of pump modifications.) Clypeal, or sucking, pumps are found in forms feeding on surface or tissue-bound fluids. Adult lepidopterans, however, possess a unique dual pump system by having both a typical clypeal pump and a pharyngeal pump with circumpharyngeal compressor muscles and spincter muscles at each end for regulation of incoming food and outgoing salivary material (Matsuda 1965).

5.5.6. Protractability/Retractability of Major Food-Reaching Mouthpart Element(s) (Character 17)

Many insects possess mouthparts whose major interacting elements with the environment are at a significant distance from the head capsule. For liquid-feeders several diverse mechanisms exist for the abaxial protraction and adaxial retraction of various probosces. Among the Lepidoptera siphon extension is caused hydraulic fluid pressure (Bänziger 1971), and recoil is effected by siphon elasticity (Eastham and Eassa 1955) and intrinsic oblique musculature (Smith 1985). In cyclorrhaphan flies, labellum extension and retraction is produced by a complex, lever-based muscular mechanism (Downes 1963, Thomson 1977). For apoid hymenopterans the glossa is deployed and withdrawn by simple glossal protractor and retractor muscles (Snodgrass 1956). Sternorrhynchous homopterans and heteropterans accomplish protraction and retraction of the beak by basal labial muscles and perhaps intersegmental beak flexion (Barth 1953). Although fluid-feeding forms such as auchenorrhynchous homopterans and nematocerous dipterans--forms that are relatively less derived within their respective order--lack proboscis-retractor mechanisms, protraction/retraction mechanisms have evolved numerous times as a way of anatomically accommodating rather bulky and long food acquisition apparati when not in use.

5.6. Character-Group IV: Clypeal Region

The clypeus represents a transitional sclerite between the head capsule proper (frons, genae, eyes, occiput, etc.) and the anatomically anteriormost sclerite, the labrum. Its major diet-related functions are (i) to provide some flexibility to the frons-clypeus-labrum series, which functions as an upper lip for the manipulation and securing of solid food and (ii) as a site of attachment for prominent cibarial dilator muscles involved in various sucking pump arrange ments in liquid feeders (Snodgrass 1947, Chapman 1982). The clypeus is thus not integrally involved in the direct operation of the mouthparts and is a relatively independent, adjacent sclerite (DuPorte 1957). It is responsible for limited labral flexibility and often contributes toward the structure of the sucking pump.

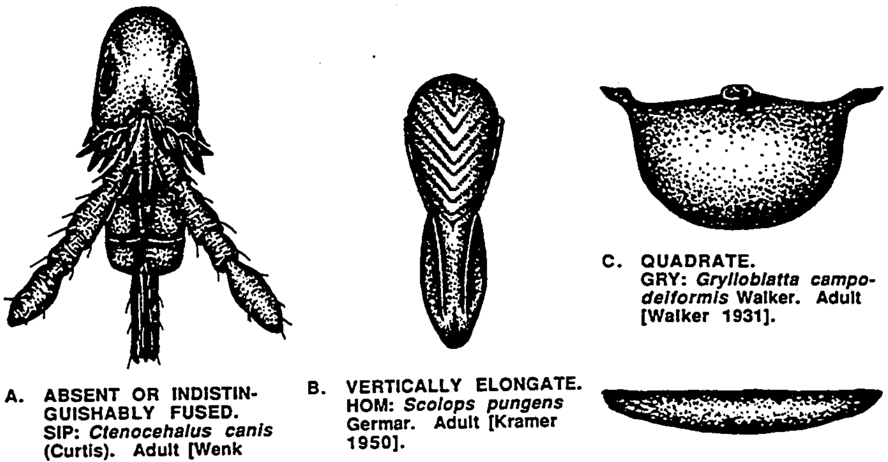
5.6.1. Shape of the Entire Clypeal Complex (Character 18)

Clypeal shape is largely determined by general head shape, mouthpart placement and the presence or absence of a clypeal sucking pump (partly after Denis and Bitsch 1973). A sagitally elongate clypeus is indicative of a laterally compressed head or of medial convergence of antennae or eyes (Denis and Bitsch 1973) (Fig. 13). By contrast, a transversely wide clypeus is associated with a dorsoventrally compressed head, wide antennae, or eyes displaced toward the genal regions, and it usually articulates with a wide labrum. This latter situation is found in hemipteroid insects, whereby the postclypeus becomes enlarged and bulbous for reception of prominent cibarial dilator muscles forming the sucking pump (Denis and Bitsch 1973). In many nonorthopteroid mandibulate insects, the clypeus is not differentiated from the frons by an epistomal suture (Snodgrass 1935). This fusion, resulting in the frontoclypeus, is mostly associated with carnivory among prognathous neuropteroid and coleopteran larvae.

5.6.2. Clypeal Subsegmentation
(Character 19)

The clypeus, as an external sclerite, may be present or absent and, if present, it may be undivided or divided into an upper postclypeus and a lower anteclypeus (Snodgrass 1935, Kukalová-Peck 1985). Alternatively, the clypeus may appear as an unusually expansive sclerite occupying most of the face in groups such as adult lepidopterans or larval dipterans, and represent either fusion to the frons (a frontoclypeus) or fusion to the labrum (a clypeolabrum). These conditions have particular, indirect consequences for feeding. With the exception of the Psocoptera, typical chewing forms that feed on solid food possess an undivided, moderately-sized clypeus. However, among the liquid-feeding hemipteroid forms, there frequently is a distinct functional subdivision of the clypeus into an inferior anteclypeus, or clypellus (Backus 1985),

SHAPE OF CLYPEAL COMPLEX



A. ABSENT OR INDISTINGUISHABLY FUSED. SIP: *Ctenocehalus canis* (Curtis). Adult [Wenk 1953].

B. VERTICALLY ELONGATE. HOM: *Scolops pungens* Germar. Adult [Kramer 1950].

C. QUADRATE. GRY: *Grylloblatta campodeiformis* Walker. Adult [Walker 1931].

D. TRANSVERSELY ELONGATE. PLE: *Perla cephalotes* Curtis. [Chisholm 1962].

FIGURE 13. Character-states of Character 18: shape of clypeal complex. Not drawn to scale.

providing a structural reinforcement of the beak base and below which houses the chamber for fluid food intake (Cobben 1978, Backus 1985). A conspicuous, bulging postclypeus (frontoclypeus of some) constitutes a massive sucking pump (Kramer 1950). In many holometabolous larvae and some adults, the undivided clypeus fuses with the frons, forming a frontoclypeus, with no indication of an intervening suture. It often appears as a flat, quadrangular plate. Such a configuration arises in prognathous, mandible-bearing forms lacking a labrum that are predatory and carnivorous in habits (Denis and Bitsch 1973). It also occurs in filter-feeding aquatic larvae who use the clypeofrontal region as a sucking pump for vacuuming detritus (after DuPorte 1957). Among adult Lepidoptera, the frontoclypeus is identified with a sucking pump for surface fluid feeding (DuPorte 1956, Ehrlich and Davidson 1961).

5.7. Character-Group V: The Labral Region

The labrum, or upper lip, is the anteriormost mouthpart region that is directly involved with food acquisition. Five principal functions are performed by the labrum. First, in mostly mandible-bearing forms feeding on solid food, the labrum is instrumental in sensing, securing, manipulation and comminution of food (Snodgrass 1960, Smith 1985). Secondly, the labrum is a support element in stylet-bearing, liquid-feeding forms (Parsons 1962, Cobben 1978). Thirdly, in conjunction with the epipharynx, the labrum forms a stylet, especially in adult blood- and sap-feeding Diptera (Bletchley 1954). Fourthly, the labral margin is extensively modified in several larval groups into filtering organs for feeding on fine-grained, particulate food (Ross et al. 1982).

Lastly, the labrum has been co-opted in various liquid-feeding groups to form a haustellum that either partly or completely encloses mouthpart stylets. These major functions are associated with various character-states in the four characters detailed in the following discussion.

5.7.1. Shape of the Labral Main Body (Character 20)

The shape of the labrum, when present, is approximately correlated with its general function. Wide or square-shaped labra are typically found in chewing, solid-food-ingesting forms such as orthopteroids, psocopterans, or adult coleopterans, whereas moderately elongate labra are used as beak braces and are identified with liquid-food feeders. Very elongate labra are stylets found in liquid-food feeders that pierce tissue.

5.7.2. Labral Subsegmentation (Character 21)

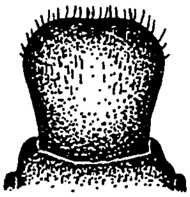
For most insects, the typical condition for the labrum is a single unit. In some forms, such as some adult Diptera and Trichoptera, it is subdivided into two segments (Crampton 1921c), a condition of unknown function. Most apterygotes possess a clypeolabrum (Francois 1959, Matsuda 1965)--a condition associated with entognathy in the same group. In various holometabolous groups, the labrum has been completely lost--for example the "*troisième group*" of larval Coleoptera in Denis and Bitsch (1973) and larval Planipennia, both of which are characterized by carnivory and jutting mandibles. In other larval forms the labrum has been replaced by a nasale--a small, triangular, acuminate projection

(Rymer-Roberts 1921), associated with carnivory-- often in piercing-and-sucking forms with suctorial, tubular mandibles.

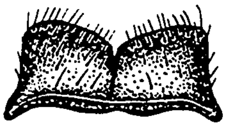
5.7.3. Modification of the Distal Margin (Character 22)

The distal labral margin displays a diverse array of modification in various larval and adult insects (Fig. 14). Although the typical condition in a generalized, orthopteroid insect is simply a straight or shallowly curvilinear margin, there have been numerous departures form the typical situation. Within orthopterids themselves, the labral margin can be medially notched, so as to channel grass blades as they are being chewed by graminivorous grasshoppers (Gangwere 1960, 1966). In adult blood-feeding black flies (Simuliidae) and sand flies (Ceratopogonidae), a well-developed spinose terminus is used for puncture of surface tissue (Wenk 1962, McKeever et al. 1988). Among aquatic, epibenthic larvae of the same family, Wallace and Cummins (1980) and Borkent and Wood (1986) have described labral fans employed for the filtering of finely particulate organic matter, and Davies (1974) has documented labral rakes used in collecting benthic detritus. For other aquatic dipteran larvae, the labrum is modified into a labral brush, with median and lateral labral hair fields used for sweeping finely divided organic detritus (Schremmer 1950a; Pucat 1965, his "browser" category; Wallace and Merritt 1980). Adult lepidopterans have a superficially similar modification, the pilifer, with setae occurring at the lateral labral margins only and used probably as a proboscis brace (Schmitt 1938). Finally, in many fluid-feeding, stylet-bearing forms,

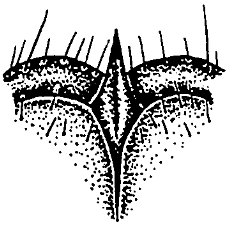
MODIFICATION OF THE DISTAL LABRAL MARGIN



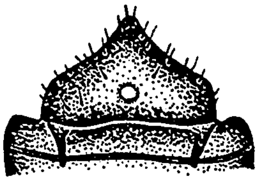
B. **STRAIGHT TO CURVILINEAR.**
ISO: *Kalotermes flavicollis* Fabricius. Adult, [Richard 1951].



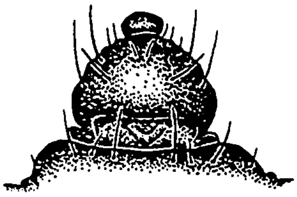
C. **NOTCHED.**
HYM: *Messor structor* Latreille. Adult alate, [Bugnion 1930].



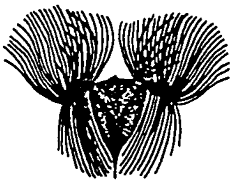
D. **MUCRONATE-ACUMINATE.**
COL: *Photurus pennsylvanica* DeGeer. Larva, [Boving & Craighead 1931].



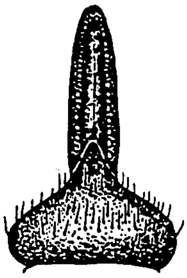
E. **TRIANGULAR-ACUTE.**
MEG: *Sialis flavilatera* (Linneaus). Larva, [Rober 1941].



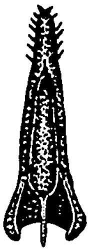
F. **LINGULATE.**
COL: *Ochthebius impressus* Marsham. Larva, [Boving & Craighead 1931].



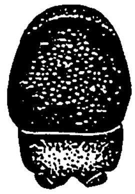
G. **PECTINATE.**
DIP: *Dixa*, sp. Larva, [Schremmer 1950b].



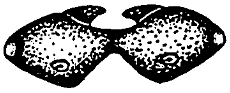
H. **BEAK BRACE.**
HET: *Velia rivulorum* Fabricius. Adult, [Servadei 1946].



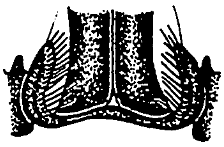
I. **SPINOSE.**
DIP: *Schizohelea leucopezia* (Meigen). Adult, [Gad 1951].



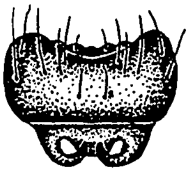
J. **MEMBRANOUS.**
MEG: *Corydalus*, sp. Larva, [Kramer 1955].



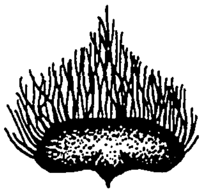
K. **APERTURATE.**
ANO: *Haematopinus suis* (Linneaus). Adult, [Stojanovich 1945].



L. **PILIFERATE.**
LEP: *Danaus archippus* Fabricius. Adult, [Kellogg 1893].



M. **UNDULATE.**
COL: *Pachorhopala jeanneli* Levasseur. Adult, [Levasseur 1965].



N. **PENICILLATE.**
EPH: *Oligoneuria*, sp. Larva, [Murphy 1922].

FIGURE 14. Character-states of Character 22: modification of distal labral margin. Not drawn to scale.

the labral margin is laterally incurved, forming an aperture for stylet protrusion. This occurs for the buccal cone of the Anoplura (Stojanovich 1945) or the labral cup of some piercing-and-sucking Coleoptera (Sen Gupta and Crowson 1973). These and other character-states illustrate the diversity of labral margins that are instrumental in capturing or otherwise processing an equal diversity of food types.

5.7.4. Labral Participation in Multielement Mouthpart Structure (Character 23)

Various functions are provided by the participation of the labrum in multielement mouthpart complexes. The participation can vary from various indirect support structures, such as a brace for a fluid-ingesting hemipteroid beak (Parsons 1959, 1962), to incorporation into a rostrum or proboscis. An example of the latter is found in seminivorous weevils, where the labrum forms a wall sclerite in the greatly elongated rostrum of the head capsule (Dönges 1954). Similarly, among the Thysanoptera, the labrum is one of several sclerites forming the wall of the mouthcone, serving as a truncate haustellum for housing and guiding the three short stylets (Reyne 1927, Mickoleit 1963). Additionally, the labrum-epipharynx constitutes one of several stylets in various dipteran and siphonapteran proboscides (Robinson 1939, Snodgrass 1959) designed for blood- or sap-feeding. A unique situation exists for aquatic odonatan larvae, wherein the labrum is a holding device for a prehensile, raptorial labial mask that is used to impale prey (Snodgrass 1954).

5.8. Character-Group VI: The "Pharyngeal" Region

The term "pharyngeal region," when applied to the cibarium, hypopharynx, or epipharynx, is a misnomer since the term "pharynx" strictly applies to the region of the stomodaeum between the cibarium (also known as buccal cavity or preoral chamber) and the esophagous (Matsuda 1965). However, because of nomen-clatural tradition, the terms "hypopharynx" and "epipharynx" are used even though both structures surround the cibarium and not the pharynx (Snodgrass 1960). The epipharynx constitutes the ventral, often membranous surface of the labrum whereas the hypopharynx is a protruding lobe separating the cibarium from the salivarium. Nevertheless, there are diverse and significant, food-related modifications of the epipharynx and hypopharynx that are related to the acquisition, processing and ingestion of food. The degree and diversity of modification of both structures and associated diets are as spectacular as the better known mandibles.

5.8.1. Cibarium Size
(Character 24)

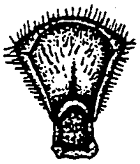
The cibarium serves as a preoral vestibule where secured food is manipulated, masticated and prepared for ingestion. Cibarial size is related to gross diet since solid-food ingesters have relatively small cibaria (Eidmann 1925) and liquid-food ingesters have potentially large cibaria because of the presence of clypeal pumps (compare Eidman 1925 with Schmitt 1938). A clypeal pump can stretch the dorsal cibarial wall to abut against the clypeal sclerite upon dilation of the clypeal muscles (Eastham and Eassa 1955). Thus this bimodal size distribution of cibaria is indicative of solid-feeding (relatively small-sized cibaria) or liquid-feeding (relatively large-sized cibaria). An intermediate-sized cibaria is allowed for in those instances where cibarial size cannot be pidgeonholed into either category.

5.8.2. Hypopharynx Type (Character 25)

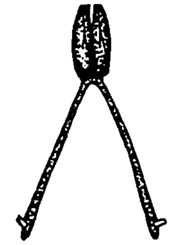
The hypopharynx in orthopteroid, coleopteran and other nominally biting-and-chewing groups serves as a tongue. According to Popham (1961), the maxillae move the food anteriorly over the hypopharynx as the mandibles are abducted. Simultaneously the hypopharynx moves forward and upwards, pushing the food towards the true mouth and between the mandibles. As a consequence of this action, the salivarium is exposed and extraoral digestive enzymes are thus spewn into the cibarium and mixed with food. As the mandibles then adduct, the maxillae are abducted and the hypopharynx is depressed to the floor of the cibarium, near the labial lower lip (see Smith 1985). This stereotyped, hard-wired response occurs in biting-and-chewing insects and, depending on food type, the hypopharynx can be variously modified to accommodate particular diets. However, in many holometabolus insects it is weakly developed or absent (Matsuda 1965).

The wealth of hypopharyngeal modification is expressed at a fundamental level in two principal structures: the lingua and the superlinguae, each of which, or both, may or may not be present (Fig. 15). The most generalized state occurs in adult orthopteroid forms, which consists of a single tonguelike process in omnivores (Blattodea)

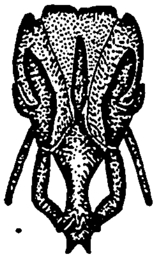
HYPOPHARYNX TYPE



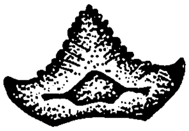
B. SPATHULATE.
ODO: *Libellula quadrimaculata* Linneaus. Adult, dorsal aspect, [Marshall 1914].



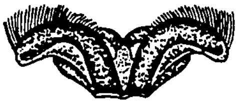
C. BILOBED.
COM: *Neanura muscorum* (Templeton). Adult, dorsal aspect, [Wolter 1963].



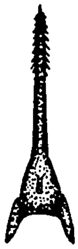
D. LINGUA + LATERAL SUPERLINGULAE.
ARC: *Machilis* sp. Adult, dorsal aspect, [Bitsch 1963].



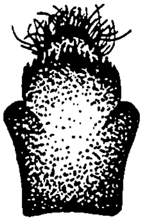
E. MUCRONATE.
COL: *Micromalthus debilis* LeConte. Larva, dorsal aspect, [Boving & Craignead 1931].



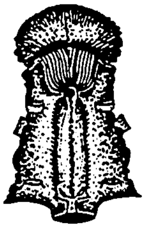
F. PECTINATE.
EPH: *Lepeorus goyi* Peters. Naiad, dorsal aspect, [Schonnmann 1981].



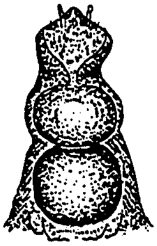
G. STYLATE.
DIP: *Promachus vertebratus* (Say). Adult, dorsal aspect, [Peterson 1916].



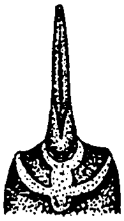
H. PENICILLATE.
DIP: *Ptychoptera*, sp. Larva, ventral aspect, [Bischoff 1922].



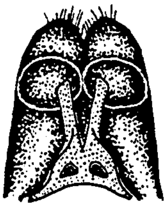
I. LABELLUM-LIKE TONGUE.
TRI: *Phryganea striata* Linneaus. Adult, anterior aspect, [Crichton 1957].



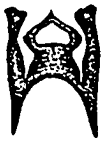
J. INCONSPICUOUS LOBE.
COL: *Dermestes nidum* Arrow. Larva, dorsal aspect, [Boving & Craighead 1931].



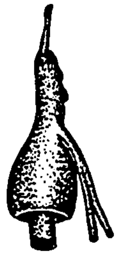
K. SPINNERET.
LEP: *Prionoxystus robiniae* Peck. Larva, dorsal aspect, [MacKay 1972].



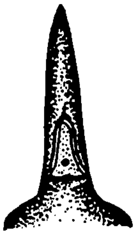
L. SUPERLINGULAE + OVOIDAL SCLERITES + SITOPHORE.
MAL: *Myrsidea cornicis* (DeGeer). Adult, dorsal aspect, [Buckup 1959].



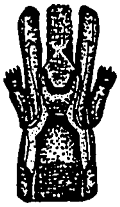
M. H-SHAPED RAMUS.
DIP: *Tanypeza longimana* Fallen. Larva, ventral aspect, [Foote 1970].



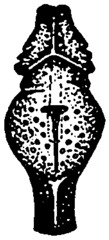
N. SALIVARY SYRINGE WITH PISTON PUMP.
HET: *Triatoma infestans* (Klug). Adult, lateral aspect, [Barth 1952].



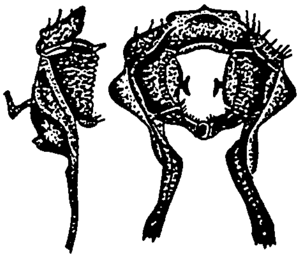
O. STYLET BRACE.
PLA: *Semidalis aleurodiformis* (Stephens). Larva, dorsal aspect, [Rousset 1966].



P. MEMBRANOUS SURFACE.
HYM: *Apis mellifera* Linneaus. Adult worker, anterior aspect, [Snodgrass 1942].



Q. BULBOUS RESERVOIR + CLYPEAL PUMP.
LEP: *Papilio demoleus* Linneaus. Adult, dorsal aspect, [Vasudeva 1956].



R. MOLARIFORM.
COL: *Dascillus cervinus* Linneaus. Larva, lateral and dorsal aspects, [Carpenter & MacDowell 1912].

FIGURE 15. Character-states of Character 25: hypopharynx type. Not drawn to scale.

or herbivores (Orthoptera). Snodgrass (1935: 114) described this structure as "a thick, sometimes irregular lobe, lying like a tongue in the preoral cavity, where it is attached to the head between the mouth and labium." Loveaux (1975) and Chapman and Thomas (1978) have described chemosensory and mechanosensory sensillae on forbivorous orthopteran tongues. Lateral superlingulae, with or without a medial lingua, have been documented by Evans (1921) in virtually every major order of insects, although superlingulae occur principally in immature forms. Among aquatic coleopteran larvae, a pectinate hypopharynx with a lingua and superlingulae occurs in many filter-feeding aquatic species (Peterson 1950, Beier 1952). In some aquatic ephemeropteran naiads, superlingulae are modified into pectinate filter-feeding organs (Schonmann 1981), whereas in others they are modified into brushlike sweeping organs used for collecting organic detritus (Murphy 1922, Brown 1961).

Parallel patterns of hypopharyngeal modification exist for aquatic mosquito larvae (Anthon 1943; Cook 1944a, 1949), although many culicids have stout denticles that assist the mastication of food by the mandibles (Harbach 1978). For larval trichopterans, lepidopterans and symphytan hymenopterans the hypopharynx and anterior labium forms a protrusible composite organ, the spinneret, used in producing silk nets for trapping detrital food in aquatic forms (Jayewickreme 1940, Fotius-Jaboulet 1961, Wallace and Merritt 1980), or for forming pupal cases or "tents" in subsocial species in terrestrial forms (Snodgrass 1928, Michener 1953).

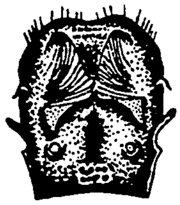
Hypopharyngeal modification is equally diverse for nonorthopteroid adult forms. In many holometabolous adults it is absent or rudimentary.

Among psocopterans and mallophagans, the hypopharynx and epipharynx are deployed as crushing or masticating organs for solid food--the characteristic mortar-and-pestle structure (Cope 1940, Symmons 1952, Hamilton 1981). Some mallophagans bear a spinose hypopharynx (Cummings 1912), presumably for macerating exfoliated dermal tissue. For some homopterans and heteropterans, the hypopharynx is a salivary syringe activated by a piston pump for the injection of lytic enzymes into the stylet canals during cibarial muscle dilation, which results in concomitant uptake of liquid food upon contraction of cibarial muscles (Parsons 1962, 1963). This structure is lined with various sensillae used for monitoring food platability (Backus and McLean 1987, Backus 1988). Piercing-and-sucking forms within dipterans bear a hypopharynx transformed into a chitinized stylet (Peterson 1916, Hu and Peng 1936), used both as a piercing organ and an injection syringe for various salivary secretions (Robinson 1939, Schiemenz 1957). The hypopharynx is also morphologically convergent on the labellum of cyclorrhaphous flies, on the Gryllidae (crickets) and adult feeding trichopterans (McAlpine 1981, Rietschel 1953, Crichton 1957, respectively), and is used for surface fluid feeding. (This structure, the haustorium, has been confusingly referred to as a "haustellum" by previous researchers [Matsuda 1965]--the latter term should be reserved for a stylet-ensheathing structure usually originating from the labium). For many typical mandible-bearing species, the hypopharynx acts as a simple molariform prominence assisting the mandibles in grinding food (Hayes 1928). In summary, with the obvious exception of the mandibles, the hypopharynx, when viewed from the perspective of diet, contains the greatest degree of structural modification of any mouthpart element.

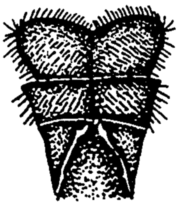
5.8.3. The Epipharynx
(Character 26)

Although the epipharynx occurs on the inferior surface of the labrum (Cook 1944a), it nevertheless is anatomically and often functionally differentiated from the labrum and has been modified into structures independent from the labrum in many forms. In unspecialized forms, the epipharynx is mostly membranous and richly supplied with gustatory sensillae and tactile setae (Packard 1898, Thomas 1966, Chapman and Thomas 1978), conforming to the overall shape of the labrum (Fig. 16). This condition exists for generalized orthopteroid (Cook 1944a) and coleopteran (Hayes 1928) forms characterized by solid-food ingestion. Among liquid-feeders, the epipharynx assumes diverse modifications, including labroepipharyngeal stylets. For many aquatic larvae, the epipharynx constitutes an integral part of the filter-straining or brush-sweeping apparatus.

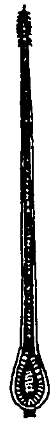
Some solid-food-ingesting insects exhibit structural modifications deviating from the generalized epipharynx described above. These include the presence of spines or coarse setae for raking detritus, which occur among aquatic mosquito larvae (Kramer 1954, Snodgrass 1959) or even among terrestrial beetle larvae feeding on carrion (Hayes 1928). Adult floricolous beetles feeding on pollen frequently have labral brushes extending to the epipharyngeal surface that are used to sweep pollen or a similar particulate material into the cibarium (Schicha 1967). A



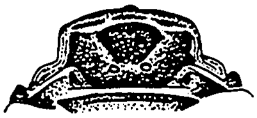
B. LINGULATE.
COL: *Glischrochilus bipustulatus* Linneaus. Larva, [Verhoeff 1923].



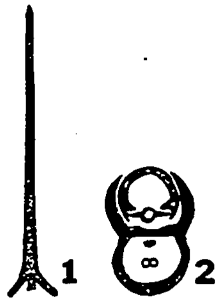
C. SETATE.
MEC: *Apterobittacus apterus* MacLachlan. Larva, [Applegarth 1939].



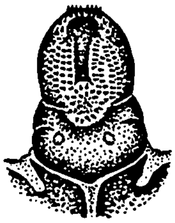
D. STYLATE.
SIP: *Ctenocephalides felis* (Bouche). Adult, [Snodgrass 1946].



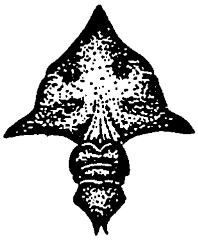
E. MEMBRANOUS.
TYN: *Thermobia domestica* (Packard). Adult, [Chaudonneret 1950].



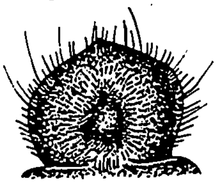
F PART OF LABRAL HAUSTELLUM.
1. DIP: *Lychnia maura* Bigot. Adult, [Jobling 1926].
2. DIP: *Hippobosca maculata* Leach. Adult, proboscis transverse section, [Dogra 1967].



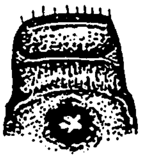
G. DENTICULATE.
ISO: *Odontotermes obesus* (Rambur). Adult alate, [Vishnoi 1956].



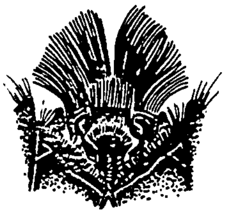
H. VENTRAL FOOD PUMP + SENSORY ORGAN + PRELABRAL GROOVE.
HET: *Notonecta undulata* Say. Adult, [Parsons 1966a].



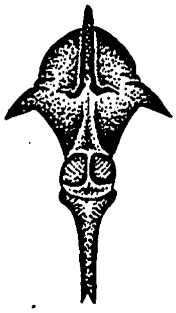
I. LOBATE WITH BODERING SETAE.
COL: *Popillia japonica* Newman. Larvae, [Hayes 1928].



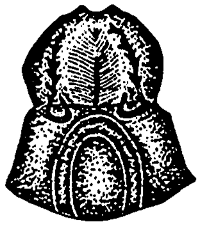
J. MOLARIFORM.
PSO: *Ectopsocus briggsi* (MacLachlan). Adult, [reconstructed from Weber 1938b].



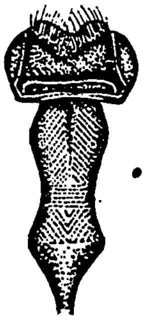
K. PENICILLATE.
DIP: *Anopheles quadrimaculatus* Say. Larva, [Farnsworth 1947].



L VENTRAL FOOD PUMP + SENSORY ORGAN + POSTLABRAL BEAK BRACE.
HET: *Ochterus foeresteri* Kormilev & DeCarlo. Adult, [Parsons 1966a].



M. PAIR OF SCLEROTIZED RODS.
BLA: *Periplaneta australasiae* (Fabricius). Adult, [Bugnion 1920].



N. V-SHAPED DEPRESSION.
HYM: *Camponotus ligniperda* Latreille. Adult worker, [Bugnion 1930].

FIGURE 16. Character-states of Character 26: epipharynx type. Not drawn to scale.

unique co-optation of the epipharynx and hypopharynx exists among the Psocoptera and Mallophaga, whereby a hypopharyngeal molariform tooth is received by a corresponding epipharyngeal concavity to form a secondary set of grinding organs in a plane 180° displaced from the mandibular articular plane--the so-called "mortar-and-pestle" apparatus (Weber 1938b, Buckup 1959). Among aquatic dipteran larvae the epipharynx, together with pectinate or fimbriate appendages, constitutes an essential part of a scraping or filtering apparatus for sweeping or straining particulate organic matter (Fortner 1937, Pucat 1965). Pao and Knight (1970) have described the complex epipharynx of a culicine mosquito larva, which is differentiated into bilaterally positioned brushes bearing pectinate hairs, more medially placed, branched, sclerotized spines, and blunt, spatulate, medially convergent "epipharyngeal processes"--each of which presumably is filtering qualitatively different suspended particle matter.

Insects feeding on fluid food possess epipharynges that can (i) serve as a beak or proboscis support, (ii) become part of the dorsal cibarial roof in a sucking pump or (iii) are converted into a labral-epipharyngeal stylet. Epipharyngeal beak braces are found among most of the Homoptera (Butt 1943) and Heteroptera (Servadei 1946, Parsons 1959), although in some forms it is supplied with sensillae used for detecting food suitability (Backus and McLean 1987, Backus 1988). For some adult Diptera and all feeding adult Lepidoptera, the epipharynx is transformed into a flexible dorsal tissue layer of the cibarium, to which sucking pump muscles are attached (Snodgrass 1959, Matsuda 1965, Schmidt 1938). Labral-epipharyngeal or epipharyngeal stylets function in piercing tissue, or they assist in withdrawing fluid food along a food canal formed in conjunction with other elongate mouthpart elements, or they accomplish both functions. Certain nematoceran, usually sanguinivorous, adult Diptera possess epipharyngeal stylets, as do the Siphonaptera (Nitzulescu 1927, Snodgrass 1946, respectively) and a few aberrant beetle groups (Vit 1977, 1981; Sen Gupta and Crowson 1973). An exceptional labral/epipharyngeal modification occurs among adult hover flies (Syrphidae) and three related adult parasitic fly families (Hippoboscidae, Nycterbiidae and Streblidae), wherein the labrum-epipharynx has been prolonged and transformed into a tubular "stylet" with terminal teeth for feeding on pollen or blood (Schiemenz 1957; Jobling, 1926, 1928a, 1929, respectively).

5.9. Character-Group VII: Mandibular Region

> La forme des mandibules varie avec le régime alimentaire...
> (Denis and Bitsch 1973: 40).

No other mouthpart element has as much well-documented functional correlation with diet as the mandibles. Mandibular morphology, dentition and, to a lesser degree, articulation and musculation, frequently have been used as features that are intimately asssociated with diet. There are three reasons for this. Mandibles are, first of all, the most conspicuous elements used directly in food processing in all biting and chewing and many piercing-and-sucking insects. Secondly, mandibles are deployed into recognizable, often distinct shapes and possess characterizable dentitions that are demonstrably analogous to vertebrate teeth. Lastly, mandibles, since they are single articulatory elements, are easily describable and can be compared among related groups with different feeding habits (Bertin 1923, Golden 1925, Isely 1944). The plethora of literature demonstrating relationships between mandibular features and diet exemplifies the importance of mandibles as clues to insect diets.

5.9.1. Mandibular Articulation
(Character 27)

The presence, number and position of condyles that articulate the movable mandible with the fixed head-capsule base reveals much about gross insect diet. Forms with a single condyle, occurring either primitively (Manton 1977) or as a secondary reversion (Dajoz 1976), have considerable mandibular movement and either feed on relatively soft food, in the case of most apterygotes, or are piercing-and-sucking forms without a lever-based muscular mechanism for protraction and retraction, exemplified by the Protura, Cerylonidae of the Coleoptera and some nematocerous Diptera. Dicondyly is a precondition for powerful, sagittally-directed power strokes necessary for the effective mastication of food (Snodgrass 1935). This situation exists for all solid food consumers, and it is typical of orthopteroids, adult coleopterans and larvae of most holometabolous larvae. The anatomical plane of articulation is parallel to subparallel to the sagittal axis in hypognathous forms, or perpendicular to the sagittal axis in prognathous forms. The occurrence of condyles that are located at the triangular base of a pyramidally shaped mandible is altered in curculionid (Coleoptera) mandibles. Curculionid mandibles are located at the terminus of an elongated rostrum and bear articulating acetabula above and below a discoid, horozontally-positioned mandible with ratchet-type teeth that are rocked by an adductor and abductor set of muscles inserted on the mandibles in the manner of "guy ropes" (Ting 1933, Dennell 1942, Brack-Egg 1973). This rotatory, mandibular motion is structured for boring into relatively hardened foodstuffs, including grain and seeds (Johnson and Lyons 1976).

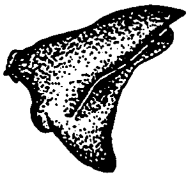
Among forms completely lacking condyles, a muscular-based lever system has originated for the protraction and retraction of often very elongate, haustellum-bound stylets for feeding on deep tissue liquids (Ekblom 1926, Newcomer 1948). Cobben (1978) has described this system of indirect stylet engagement for numerous heteropteran species, virtually all which bear a triangular-shaped "mandibular sclerite," or lever, that is attached to protractor muscles originating from the head capsule or a tentorial arm and is also attached by tendons to the stylet base. This lever magnifies muscular movement during downward stylet engagement. Upward stylet degagement is effected by a direct retractor muscle that inserts on the stylet base and originates on the head capsule or a tentorial arm. A similar mechanism exists for the liquid-feeding Homoptera (Spooner 1938, Bourgoin 1986b), although for the dominately "punch-and-sucking" Thysanoptera, stylets are protracted and retracted by direct muscular attachments to the tentorium (Reyne 1927).

5.9.2. Mandibular Type
(Character 28)

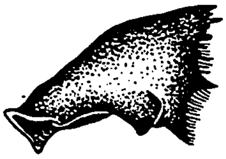
According to Denis and Bitsch (1973: 31), "It has been shown that the shape of the mandibles varies according to the [taxonomic] order and diet of the insect." When the totality of insect mandibular form is considered, it is evident that there are at least as many mandible types as insect diets. Eighteen distinctive, major mandible types have been determined in this study (Fig. 17), most which have strong associations with particular dentitions (Character 29). Some of these mandible types are uncommon or rare.

As an assemblage, mandible types are very diverse and range from typical orthopteroid, pyramid-shaped forms, to more two-dimensional, raptorial "talons", to tubular piercing hooks and prolonged, edentulous stylets. Mandibular shape and dentition can be quite variable within related genera (Narayanan et al., 1955) or even among different castes of the same species (Wheeler 1927, Hare 1937, Wilson 1971).

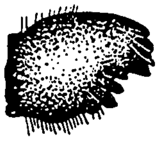
Mandibles used as biting-and-chewing organs are robust, usually dentate and dicondylic. A very common mandibular type is the pyramid-shaped, generalized form found in most orthopteroids and coleopterids, used for solid-food ingestion (Crampton 1921a). Occasionally this mandible type is differentiated dentally for use in more restricted diets, such as forbivory, graminivory, insectivory or necrovory (Bertin 1923, Isely 1944, Chapman 1964). Another common form is the sickle-shaped, falcate type used by predatory forms such as tiger beetles (Cicindelidae; Evans 1965a, 1965b), worker-caste ants (Wheeler 1927, Barth 1960) or some stonefly naiads (Hoke 1924, Hansen 1946). Among tiger beetles, Pearson (1988, oral presentation) has established a strong correlation between mandible length and prey length ($R = 0.943$), indicating a functional effect of mandibular structure on prey capture. Rarely, falcate mandibles are employed for other functions, such as necrophagy by skin beetles (Trogidae; Bertin 1923) or colony defense by



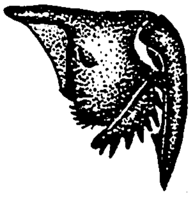
B. TRIANGULAR.
MAL: *Pseudomenopon pilosum* (Scopoli). Adult, [Haub 1967].



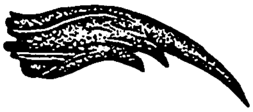
C. SECURIFORM.
EPH: *Chloeon dipterum* Linneaus. Naiad, [Brown 1961].



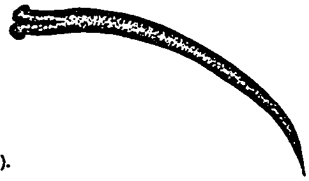
D. QUADRANGULAR.
ORT: *Melanoplus angustipennis.* Adult, [Gangwere 1965].



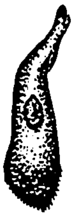
E. MAXILLO-MANDIBULAR COMPLEX.
DIP: *Rhagio scolopaceus* (Linneaus). Larva, [Roberts 1969].



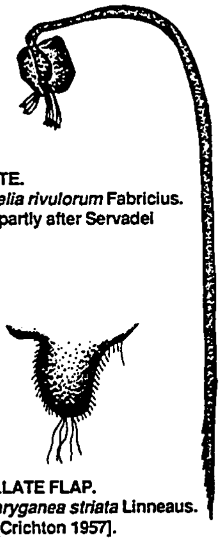
F. MODERATELY FALCATE.
MEG: *Sialis flavilatera* (Linneaus). Larva, [Rober 1941].



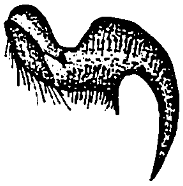
G. EXTREMELY FALCATE.
MEG: *Corydalus cornuta* (Linneaus). Adult male, [partly after Kellogg 1902].



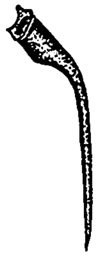
H. ENSIFORM.
DIP: *Simulium erythrocephalum.* De Geer. Adult, [Grenier 1959].



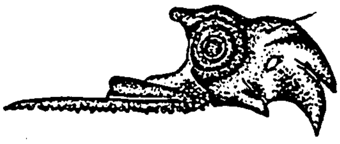
I. STYLATE.
HET: *Velia rivulorum* Fabricius. Adult, [partly after Servadei 1946].



J. TUBULATE/FALCATE.
COL: *Lampyris noctiluca* Linneaus. Larva, [Vogel 1915].

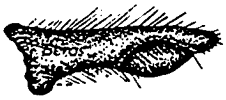


K. ACICULATE.
THY: *Chirothrips hamatus* (Trybom). Adult, [Jones 1954].

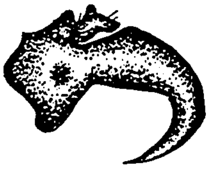


L. RATCHET-SHAPED.
COL: *Cionus scrophulariae* Linneaus. Adult, [Donges 1954].

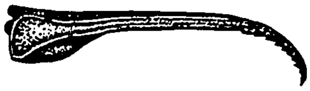
M. LAMELLATE FLAP.
TRI: *Phryganea striata* Linneaus. Adult, [Crichton 1957].



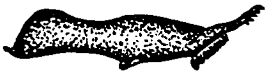
N. EXCAVATE.
HYM: *Apis mellifera* Linneaus. Adult worker, [Nedel 1960].



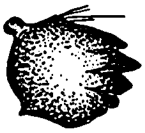
O. HAMATE.
DIP: *Cephenomyia auribarbus* Meigen. Larva, [Cameron 1932].



P. GROOVED-FALCATE.
PLA: *Neurorthus fallax* (Rambur). Larva, [Zwick 1967].



Q. PROLONGED.
COM: *Tomocerus plumbeus* Linneaus. Adult, [Hoffmann 1908].



R. PALMATE.
LEP: *Carpocapsa pomonella* Linneaus. Larva, [Peterson 1948].

FIGURE 17. Character-states of Character 28: mandibular type. Not drawn to scale.

worker worker caste termites (Emerson 1965, Wootton 1984). Extremely falcate, almost grotesque, mandibles are not used for feeding and are employed for clasping females during copulation by adult male dobsonflies (Matsuda 1965) and probably by adult males of a genus of katydids (Gurney 1950).

Variations of the generalized biting-and-chewing mandible are frequently structured to perform specific functions on distinctive diets. For example, piercing, entognathous insects possess long, quadrangular mandibles that can slide up-and-down in a single, mandibular articular socket (Borner 1909, Bitsch 1963). Pterygote modifications include mandibles with flexible blades for scraping and molding dung in scarab beetles (Bertin 1923, Hata and Edmonds 1983); mesially excavated mandibles in adult hymenopterans that are used for molding mud or wax in the construction of dwellings (Nedel 1960); the ratchet-toothed, discoid mandibles of weevils, used for boring or grinding through hardened foods (Johnson and Lyon 1976); and the distally expanded, pectinate or fimbriate mandibles of mayfly naiads or fly larvae, used for filtering or scraping food (Strenger 1953; Brown 1961; Craig 1974, 1977). Colless (1977) has described mandibles from dipterans that bear profuse, long setation and are deployed into a hemispherical cephalic fan that is used as a sieving structure.

A major modification of the falcate mandible occurs among several groups of holometabolous larvae who transform the mandible into a suctorial, tubular piercing device used in sucking out the liquified contents of arthropod prey items. This general modification has assumed at least three major variations, including (i) the tubulate mandibles of seven families of larval Coleoptera (e.g. Vogel 1915, Blunck 1918, Bitsch 1966, Honomichl 1975), (ii) the tubulate mouthhooks of some cyclorrhaphan flies (Teskey 1981d) (iii) and the participation of the mandible and maxillary lacinia to form the lumen of the mandibulo-maxillary complex in all Planipennian larvae (Principi 1954, Rousset 1956, Wundt 1961). Functionally, these mouthpart types are convergent on adult stylet-bearing forms engaging in insectivory.

Elongate, linear mandibles designed for nonhaustellate piercing-and-sucking and withdrawing of fluid food occur in many holometabolous groups and even in orders considered as typically nonpiercing. Among the typically mandibulate Coleoptera, four families have exposed, piercing mandibles derived from typical biting-and-chewing ancestors (Besuchet 1972, Dajoz 1976, Crowson 1981). Similarly, one siphon-bearing family of Lepidoptera, the Noctuidae, contains several genera of blood- and fruit-feeders with a galeal siphon modified into a monostylate piercing instrument (Darwin 1875, Srivastava and Bogawat 1969, Banziger 1967-1980). The apterygote Protura also bear nonhaustellate stylets, with the major difference of being housed in a buccal sac (Francois 1959). In haustellum-bearing groups, mandibles, when present, can take the form of small, relatively short, stilleto-shaped stylets used in puncturing shallow tissue, or they can be very long, gracile stylets that can be coiled like a watchspring in the cephalic capsule upon retraction (Spooner 1920, China 1931). Among the former, the Thysanoptera and some nematocerous Diptera are good examples (Peterson 1915, Risler 1957, Wirtz 1987a), bearing mandibles similar in shape to various nonhaustellate piercing groups, and are used to punch into substrates such as pollen, seeds, or shallow dermal tissue (Kirk 1984, 1985; Mound, in litt., 1986). By contrast, deep-tissue feeding is prevalent in the Homoptera, Heteroptera and in various nematocerous and brachycerous Diptera. The Homoptera and Heteroptera are characterized by noninterlocking, opposable, mandibular stylets working in conjunction with similarly long, adjacent maxillary stylets housed in a completely encircling, segmented labial beak (Parsons 1959, Cobben 1978, Wirtz 1987a). Many adult Diptera are also deep-tissue feeders and are similarly characterized by noninterlocking, opposable mandibles, but they are loosely housed in a partly encircling, unsegmented, labral-labial or entirely labial proboscis (Vogel 1921, Whitfield 1925, Jobling 1933, Grenier 1959). In some relatively shallow-feeding dipterans the mandibles are wide, serrated blades (Jobling 1928, McKeever 1986, McKeever et al. 1988) that are used for cutting and slashing surface tissue rather than piercing action of deep-tissue feeders. A unique situation exists for anoplurans, which bear prolonged, fixed mandibles that are nonarticulating, unmusculated and U-shaped in cross-section (Hirsch 1987). Anopluran mandibles are used as stylet guides for the protraction and retraction of the hypopharyngeal and labial stylets (Hirsch 1986).

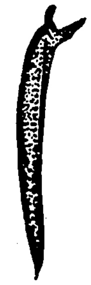
5.9.3. Mandibular Dentition
(Character 29)

Mandibular dentition, as it relates to insect diet, has been extensively investigated. Numerous studies involving (i) natural historical field observation (Narayanan et al. 1955, King and Thompson

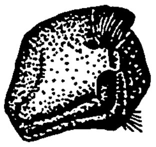
1958), (ii) laboratory and field examination of associations between dentition and diet (Isely 1944; Gangwere 1965, 1966, 1972; Paranjape 1985) and (iii) functional morphological explanations of the relation ship between teeth morphology and diet (Cobben 1978, Evans and Forsythe 1985), have all demonstrated a close correspondence between dentition and diet. This diversity of approaches and an eclectic sampling of insect groups in assessing the relationship between dentition and diet indicates that, for many insect groups, diet can be closely approximated by an examination of tooth location and morphology. (Of any character in the data-set, mandibular dentition--like its parallel among vertebrate jaws--has allowed for numerous approaches for the study of the association between mouthparts and diet.)

Insect dentition consists of two general elements: proximal molars and distal incisors (Fig. 18). Particularly prominent, acuminate incisors are often termed canines. Canines may occur as prominent teeth within a multitoothed mandible, or they may consist of a single, prominent "tooth" comprising a major part of the mandible (Golden 1925). Other elements of the dentition include rigid, elongate, movable processes, brushes (brustia) and isolated or spaced setae forming straining or sweeping apparati (see Knight [1971] for examples among culicid larvae). Also important are various chemosensory and mechanosensory sensillae, positioned at gustatorily strategic locations on the mandible (Louveaux 1972, Chapman and Thomas 1978).

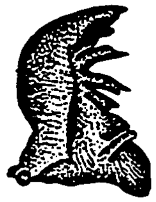
The best examples of dentition/diet associations occur in studies of the Orthoptera and Coleoptera. For the Orthoptera, Isely (1944) examined 89 species of North American Acrididae and Tettigonidae and



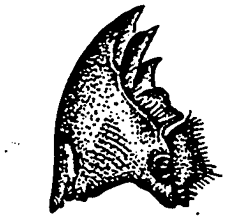
B. **EDENTATE.**
DIP: *Tabanus atratus* Fabricius. Adult female, [Snodgrass 1943].



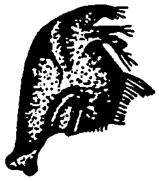
C. **MOLAR REGION DOMINANT.**
PHA: *Diaphaneromera femorata* (Say). Adult, [Walker 1933].



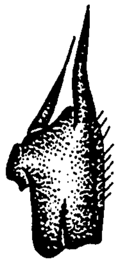
D. **INCISIFORM REGION DOMINANT.**
COL: *Hydrophilus piceus* Linneaus. Adult, [Golden 1925].



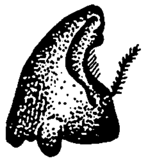
E. **MOLAR AND INCISOR REGION DOMINANT.**
BLA: *Periplaneta australasiae* (Fabricius). Adult, [Mangan 1908].



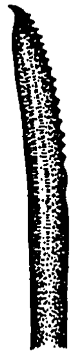
F. **PECTINATE.**
EPH: *Siphlonurus aestivalis* Eaton. Naiad, [Schonmann 1981].



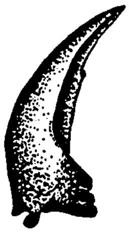
G. **CHELATE.**
COL: *Axiocerylon cavicolle* Grouvelle. Adult, [Sen Gupta & Crowson 1973].



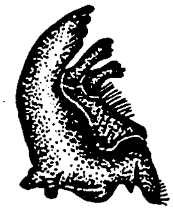
H. **PROSTHECATE.**
COL: *Limnius troglodytes* Gyllenhal. Larva, [Boving & Craighead 1931].



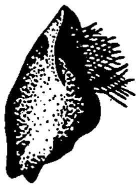
I. **SERRATE.**
HET: *Triatoma maculata* Erichson. Adult, [Cobben 1978].



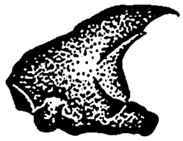
J. **PROMINENT CANINE + MOLAR REGION.**
COL: *Cantharis* sp. Larva, [Peterson 1951].



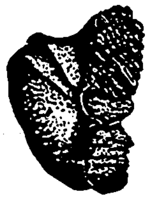
K. **LACINIA MOBILIS DOMINANT.**
EPH: *[illegible] pugnax* LeConte. Naiad, [Snodgrass 1950].



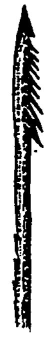
L. **PENICILLATE.**
TRI: *Drusus trifidus* Mac Lachlan. Nymph, [Fotius-Jaboulet 1961]



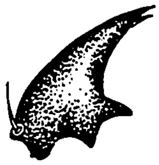
M. **PSITTACIFORM.**
MAL: *Laemobothrium gypsis* Kellogg. Adult, [Snodgrass 1905].



N. **LOPHODONT.**
COL: *Melolontha vulgaris* Fabricius. Adult, [Bertin 1923].



O. **BARBED.**
HET: *Hydrometra stagnorum* Linneaus. Adult, [Cobben 1978].



P. **PROMINENT CANINE ONLY.**
COL: *Chilocorus bivulnerus* Mulsant. Larva, [Gage 1920].

FIGURE 18. Character-states of Character 29: mandibular dentition. Not drawn to scale.

found seven distinct modes of dental and mandibular modification, involving molar spacing, molar and incisor sculpture, the degree and type of molar-cusp development and mandibular length. His corresponding diet categories were forbivory, graminivory, herbivory (intermediate between the former two), carnivory, seminivory, florivory/forbivory and lignivory. In an earlier study, Isely (1938) also found distinct associations between diet and diet breath. Chapman (1964) and Patterson (1983) produced results consistent with Isely's classification, distinguishing three basic diet and dentition types--forbivory, graminivory and herbivory--among more taxonomically limited data-sets. Gangwere (1960, 1965, 1972), in an independent study of 68 species of Michigan Orthoptera, arrived at practically identical mouthpart/diet associations as Isely (1944), using mandibular as well as other mouthpart data. In a brief study of Argentinian orthopterans, Liebermann (1968) used cusp morphology to distinguish between forbivorous and graminivorous dentitions. These results were repeated by Williams (1954) in a study of *Locusta*, *Schistocera* and eleven British acridids. Golden (1925), in a coarser-grained but taxonomically more comprehensive study, was able to differentiate omnivorous, herbivorous and carnivorous dentitions among members of the Orthoptera, Blattodea, Mantodea, Phasmida, Dermaptera and Odonata. As a rule, carnivorous species lack grinding molar areas and bear acuminate incisors (Watson 1955; Popham 1959, 1962; Matsuda 1965), whereas herbivorous species *sensu lato* bear well-developed molar grinding surfaces (Pradhan 1938, Butt 1951) at the expense of incisor development, and omnivorous and some leaf-cutting species possess a battery of both cusped molars and well-developed incisors (Bertin 1923).

Major dentition/diet patterns have also been documented for adult Coleoptera. For ladybird beetles (Coccinellidae), herbivorous species are characterized by an incisor region bearing a few blunt teeth used for scraping surface tissue and a molar region consisting of grinding teeth with uniformly distributed tubercles (Pradhan 1938, Butt 1951). Among the scarab beetle genus *Melolontha* (Scarabaeidae), molars bear a lophodont dentition, with the carina of one molar occluding with the sulcus of the opposite mandible (Osterwald 1954). In forms with pronounced extraoral digestion such as the Carabidae and Silphidae, molar dentition is absent or minimal, and the distal mandible region is characterized by a single, pronounced, often falcate tooth bearing accessory denticles on the mesal, medial surface (Pauly 1915, Golden 1925). For some Scarabaeoidea, Bertin (1923) and Golden (1925) evaluated mandibular dentition for 20 genera, concluding that five major dentition/diet associations exist: namely forbivorous, lignivorous, florivorous, stercovorous and necrovorous types. These types were morphologically characterized by combinations of molar area, incisor sharpness, incisor shape and length, mandibular hirsuteness, the presence of a flexible incisor scraper, and patterns of maxillary galeal modification. Beetle dentition is also characterized by variously covered articulatory processes, termed prosthecae or laciniae mobili, employed for moving food from the cibarium to the oesophagus (Blackwelder 1934, Smith 1985). Frequently these processes are used in conjunction with labral and maxillary brushes for pollen feeding among floricolous forms (Schicha 1967, Barth 1985).

Among larvae, dentition patterns are equally diverse. Dentate forms possessing falcate, tubulate or nontubulate mandibles include among the Coleoptera, the aquatic Dytiscidae (Blunck 1918), Hydrophilidae (Moulins 1959, Bitsch 1966), Gyrinidae (Bitsch 1966, Honomichl 1975), terrestrial Lampyridae (Vogel 1915, Gardner 1946) and Cantharidae (Böving and Craighead 1931, Bitsch 1966). Similar modifications are found in all Plannipennia larvae (see Sundermeier [1940] and Zwick [1967] for examples) and most larvae of cyclorrhaphan Diptera (Teskey 1981d). Other carnivorous forms such as the Silphidae possess falcate mandibles, but with acuminate denticles (Lengerken 1938). Herbivorous larvae, especially caterpillars (Lepidoptera), possess triangular-shaped mandibles with several palmately distributed, terminal incisors (Djamin and Pathak 1967, Lawrence 1977; see Peterson 1948 for numerous examples). Deciduous cusps of apparently unknown function have been described by Wilcox and Baker (1935) in larvae of curculionid coleopterans. For aquatic immatures, ephemeropteran, plecopteran, trichopteran and dipteran larvae possess two major dentition types: forms with distal mandibular brushes for sweeping organic debris into the cibarium (Hartland-Rowe 1953, Froelich 1964 for Ephemeroptera; Hoke 1924, Chisholm 1962 for Plecoptera; Slack 1936 for Trichoptera; Chance 1970, Gardner, Nielsen and Knight 1973 for Diptera), and forms bearing pectinate, often radiate spines or setae for filtering suspended particulate food (Brown 1961, Schonmann 1981 for Ephemeroptera; Moulins 1968 for Plecoptera; Davies 1974, Craig 1974 for Diptera). Lawrence (1977) provides a cursory survey variation in mandible dentition among herbivorous (*sensu lato*) coleopteran larvae.

Mandibular stylet dentition among piercing-and-sucking forms is much simpler in variety and straightforward in interpretation. Many, relatively short mandibular stylets are edentate and are used to pierce skin or puncture hardened tissue (Smith 1985). This occurs in the Protura, Anoplura, Thysanoptera and some Diptera. Other forms use a cut-and-slash approach for surface feeding and bear broad blade-like mandibles with prominent serrations (McKeever 1986, McKeever et al. 1988). Relatively long mandibular stylets are often serrated on one or two sides (Ekblom 1926; Wundt 1961, Cobben 1978) or have barbed extremities, forming an armature of acuminate, recurved denticles encircling the distal stylet region (Darwin 1875, Gordon and Lumsden 1939, Waldbauer 1962, Wirtz 1987a). In deep-tissue-feeding dipterans it is the maxillary stylets that are directly engaged in piercing and cutting tissue (Griffiths and Gorden 1952), and the mandibular stylets enter an already-formed wound (Smith 1985). For deep-tissue-feeding Homoptera and Heteroptera, the sequence of piercing is the opposite (Cobben 1978). Among aphidid homopterans and glossinid dipterans, there is considerable control of stylet movement. For example, Miles et al. (1964) have documented the existence of a proteinaceous tubular sheath, secreted by the salivary gland, into which stylets are deployed in two aphid species; Gordon et al. (1956) have established that directional stylet control is essential for blood-vessel location for tsetse flies. Various homopteran species have the ability either to pierce cells or to follow intercellular paths along the middle lamella (McAllan and Adams 1971; Pollard 1969, 1973).

5.9.4. Musculation and Mandibular Motion (Character 30)

Mandibular motion and associated musculation is a characteristic associated with gross diet type. Forms without mandibular motion or musculation undoubtedly are nonfeeding. Species with a vertical power stroke perpendicular to the sagittal plane and characterized by protractor and retractor muscles are liquid-feeding forms. Typical biting-and-chewing forms function with mandibular motion effected by adductor and abductor muscles that induce power and recovery strokes either perpendicular to the sagittal plane in hypognathous forms or parallel to the sagittal plane in prognathous forms. A special case exists for those forms, principally cyclorrhaphan fly larvae, with modified "mandibles"--mouthhooks--which are protracted and retracted in a semicircular, vertical plane (Ludwig 1949, Roberts 1971) in a motion akin to that of piercing stylets. This derived condition represents a rotation of the mandibular muscle origins from a central position to a more lateral position on the cephalic capsule, thus transforming an orthopteroid-type larval adducting/abducting musculature into, in effect, a protracting/retracting musculature typical of most piercing-and-sucking, stylet-bearing insects.

5.9.5. Mandibular Participation in a Multielement Mouthpart Structure (Character 31)

For those adult multielement mouthpart complexes where the mandibles form an essential component, mandibular co-optation has been predominantly for the uptake of liquid foods. In almost all multielement mouthpart complexes, mandibles have been transformed into stylets for piercing tissue or have been involved in the formation of a stylet-based food canal for liquid-food ingestion. A single mandible in conjunction with two maxillary stylets has formed an efficient "punch-and-suck" mechanism in the Thysanoptera (Heming 1978). Four elongated, often barbed or serrated stylets--two internal, piercing mandibular stylets and two external, "anchoring" maxillary stylets--form the highly stereotyped piercing-and-sucking mechanism of the Homoptera and Heteroptera (Cobben 1978, Wirtz 1987a). This apparatus is enclosed by a three- to four-segmented haustellum (Smith 1985) colloquially known as a beak. By contrast, various Diptera and Siphonaptera exhibit a nonsegmented, labial haustellum characterized by the assembly of from two to six noninterlocking stylets that are entrained by a viscous fluid causing adherence of the stylets to one another during feeding (Robinson 1939, Schiemenz 1957). Such a proboscis is informally described as "fasiculate" because of the separation of stylets during times of nonfeeding. In several, mostly mandibulate, groups, stylus-like mandibles are frequently co-opted with maxillae and occasionally with hypopharyngeal or epipharyngeal stylets to form nonhaustellate mouthparts used for piercing-and-sucking. These forms feed on plant juices, such as the orthopteran Cooloolidae (Rentz 1980, 1987), coleopteran Sphaeriidae (Crowson 1981), Rhysodidae (Pauly 1915), Eucinetidae (Vit 1977, 1981), Corylophidae (Pakaluk 1987) and Cerylonidae (Dajoz 1976); blood, such as the mallophagan Ricinidae (Clay 1949); and soft interstitial soil invertebrates, such as the collembolan Neanuridae (McNamara 1924) and the Protura (Sturm 1959).

The only larval mouthpart co-optation involving the mandible is the characteristic mandibulomaxillary complex of the Planipennia. In this apparatus the prominent, falcate mandible bears a longitudinal furrow throughout its length and is capped by an adjacent, complementary maxillary lacinia. Both structures conjointly form a lumen for the extraction of liquid food and/or injection of lytic enzymes into insect prey items (Griffiths 1980). Adult mandibular co-optation occurs in the formation of a cephalic rostrum. A rostrum is a prolongation of facial and fixed mouthpart sclerites distally to form a pronounced, cylindrical extension of the face beyond the bulbous head capsule that bears terminal mouthparts. This feature is most evident in the Mecoptera and Curculionoidea (Coleoptera). Both groups however are rostrate for different reasons--the Mecoptera because of their habits of feeding deep into carrion (Hobby and Killington 1934) and most Curcurlionoidea because of their ability to bore or chew in nominally inacessible, deep tissues of plants (Crowson 1981).

5.10. Character-Group VIII: The Maxillary Region

Like the mandibles, the maxillae are paired elements but, unlike the mandible, each maxilla consists primitively of five separate elements: two, mostly fixed, basal elements (cardo and stipes) and three movable appendages (galea, lacinia and palpus). Thus the maxilla, as a multielement structure, bears elements that can be modified in various combinations--either within the maxillary complex or between the maxillary complex and adjacent mandibular or labial mouthpart regions.

Each of these three general types of co-optation is represented by structural modifications in a major insect group.

When considered in its total range of structural deviation, the maxilla exhibits three major morphological trends. These are (i) a generalized, unmodified, maxillary form represented by virtually all orthopteroid, adult neuropteroid and adult coleopterid insects, (ii) a tendency toward maxillary reduction among many holometabolous larvae and most hemipteroids and (iii) various combinations of intramaxillary elements or elements between the maxilla and adjacent mouthpart region in holometabolous adults to form feeding organs for liquid or exceptionally hard foods. An account of the generalized condition is given in section 3.4.4 (but also see Bugnion [1920] and Popham [1961]). Examples of reduction occur among hymenopteran larvae, wherein the galea and lacinia often fuse to form a stout, generalized lobe and the palpus is shortened in length and segment number into a short stub (Das 1938, Peterson 1948). For most hemipteroids, the only major demonstrable structures present are the maxillary stylet, the maxillary stylet lever and the maxillary plate; the galea, palp and often the stipes are absent (Spooner 1938, Cobben 1978). (In the Anoplura, galeal structures are used as a stylet-channelling device [Wirtz 1987a].)

Numerous independent morphological trends occur in the maxilla of holometabolous adults. These include the conjoining of galeae to form a maxillary siphon among adult Lepidoptera and meloid Coleoptera (Eastham and Eassa 1955, Grinfel'd 1975), the elongation of maxillary laciniae to form stylets in various haustellum-bearing and haustellum- lacking proboscides (Peterson 1916, Francois 1959, Cobben 1978) and the formation of the maxillolabial complex in bees (Snodgrass 1935). The maxillolabial complex is characterized by long, semicylindrical, maxillary galeae that participate in the formation of a tubular structure which, in conjunction with labial palps, is used for ingestion of fluid (Harder 1982). Among all of these and other maxillary modifications of the adult Holometabola, it is the galeae and the laciniae that are the major participants of morphological innovation. Their transformation includes structures modified as tubes, stylets and glossa-clasping devices. The fixed maxillary elements, stipites and cardines, by contrast, have been incorporated as wall sclerites in various rostra (McClenahan 1904, Otanes 1922).

5.10.1. General Condition of the Stipes (Character 32)

Stipital development and length is a general function of the prolongation of the maxillary complex. In some solid-feeding, hypognathous and prognathous forms, stipital extension is indicative of either an abaxially prolonged maxilla as an independent region, or the stipes contributes to wall formation of an interregion multielement proboscis with terminal movable mouthparts. Such forms possess stipites that are rectangular to rod-shaped, indicative of maxillary elongation. Examples include the Nemopteridae of the Planipennia (Parker 1987), the Curculionidae of the Coleoptera (Pajni and Chhibba 1972), most adult Mecoptera (Hepburn 1969) and the Apoidea of the Hymenoptera (Plant and Paulus 1987).

Insects with maxillae relatively proximal to the head capsule bear stipites that are squarose to transversely elongate in shape. Examples include virtually all orthopteroid, adult coleopterid and nonapoid adult hymenopterid insects (for descriptions of this maxillary condition, see Levereault [1936] for the Mantodea, Butt [1944] for the Coleoptera and Matsuda [1957] for the Hymenoptera). Among most liquid-feeding hemipteroid taxa, the stipites contribute toward formation of the maxillary plate (Matsuda 1965)--a sclerite located on the inferior aspect of the cephalic capsule (Parsons 1962). Some larval and adult Diptera possess stipites that are uniquely attached to their adjacent mandible, or both stipites are fused (Gad 1951, Valliant and Delhom 1956)--structures with unknown associations.

5.10.2. Maxillary Main-Body Segmentation (Character 33)

The differentiation of the maxillary main-body--the stipes and cardo--into supernumerary sclerites is probably an indication of the articulatory freedom of the maxilla for manipulation and mastication of food. Subdivision of the main-body into four sclerites occurs in solid-food-ingesting forms, namely in virtually all orthopteroid groups and among many coleopterid and hymenopterid groups. Main-body partitioning into three sclerites also occurs in mandibulate groups, particularly plecopteran naiads, trichopteran and lepidopteran larvae, and certain coleopteran larvae and adults. Only hemipteroid taxa possess a uniform reduction of the stipites and cardines into one sclerite only, associated with overall maxillary reduction (only the lacinial stylet is conspicuously present) and transformation of the mouthparts into piercing stylets. The morphologically nonderived condition, an undivided stipes and an undivided cardo, occurs in adults and includes both biting-and-chewing forms such as neuropteroids, many coleopterans, mecopterans and in surface-feeding forms, such as trichopterans, lepidopterans and hymenopterans. There appears to be no association between the presence of the underived condition and feeding type.

5.10.3. Maxillary Appendages (Character 34)

The presence and number of maxillary appendages, i.e. the galea, lacinia and palpus, is broadly associated with diet. The most taxonomically widespread condition is the presence of all three appendages--a feature found in most solid-food-feeding insect orders, especially among the apterygotes, orthopteroids, Psocoptera, Mallophaga, Coleoptera, Mecoptera and Hymenoptera. This character-state is associated with forms that bear generalized to specialized biting-and-chewing mandibles. Of the ten remaining character-states, nine are combinations that represent anatomical reduction. Appendicular reduction can be condensed into three patterns: (i) appendage "loss" by interappendicular coalescense, such as fusion of the galea and lacinia to form a mala, (ii) actual appendage loss and (iii) dimunition in size of all appendages and their eventual disappearance. While various groups of immatures (especially holometabolous larvae) characterize many of the character-states, other character-states are dominated by various adult species that have eliminated a particular maxillary element to accommodate the specialization of other, adjacent elements. In cases involving nonfeeding forms, there has been drastic downsizing of all movable maxillary elements, approaching vestigiality or even total absence.

Maxillary appendage reduction among biting-and-chewing immature forms has occurred principally by formation of a linguloid mala from fusion of the galea and lacinia (see Das 1938 and Peterson 1948, 1950 for numerous examples). This reduction has occurred among detritivorous ephemeropteran naiads, carnivorous odonatan naiads, dominately carnivorous and fungivorous coleopteran larvae and many detrivorous and carnivorous dipteran larvae, among other groups. It is rarely present in herbivorous immatures. Some dipteran larvae similarly exhibit development of a mala, but lack a palpus (see Hennig 1948-1952 for documentation). Herbivorous lepidopteran larvae and most dominately carnivorous, endoparasitic hymenopteran larvae bear a maxilla devoid of a lacinia (Jayewickreme 1940, Short 1952, MacKay 1972). Obligately carnivorous planipennian larvae exhibit complete suppression of the galea and palpus, with the lacinia forming a conspicuous sickle-shaped cover for the channeled, piercing mandible (Rousset 1966). Likewise, galeal and palpal supression is repeated in immature and adult Homoptera and Heteroptera, wherein the lacinia becomes a prolonged, sclerified stylet moving in conjunction with mandibular stylets (Muir and Kershaw 1911, Cobben 1978). Maxillary reduction also occurs in several genera of adult Noctuidae (Lepidoptera), which are characterized by the absence of laciniae and palps and the presence of a galeal siphon transformed into a semirigid, distally sclerified and barbed stylet for feeding on blood or on fluids deep in fruit tissue (Banziger 1967-1980).

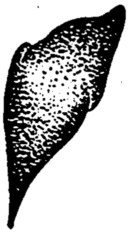
Many other adult insects have variously transformed laciniae into stylets while retaining other maxillary appendages. The Thysanoptera possess a stiletto-shaped lacinial stylet, a palpus and a galea that forms a region of the mouthcone wall (Peterson 1915, Heming 1978). Most piercing- and-sucking dipterans lack galeae but retain their lacinial stylets and palps, especially among the more derived Nematocera and Brachycera (Peterson 1916, Hoyt 1952). By contrast, virtually all adult lepidopterans lack laciniae and bear prominent galeae conjoined into a flexible siphoning tube for fluid-feeding (Eastham and Eassa 1955; Ehrlich 1958a, 1958b). Apoid hymenopterans, however, possess rather small, lobate lacinia and bladelike, amplexiform galeae (Saunders 1891, DeMoll 1908) employed for clasping the glossa as it is withdrawn with liquid food (Snodgrass 1947). Almost all of the above-mentioned examples can be characterized by a discrete combination of maxillary appendages, each of which is associated with a distinctive feeding style and often a categorizable diet.

5.10.4. Maxillary Palpus Segmentation (Character 35)

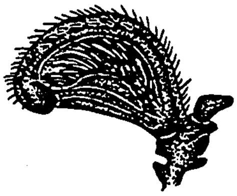
When considering the total array of maxillary palp segment number (Fig. 19), four general trends are evident. The first trend is retention of the probably primitive five-segmented condition (palpifer excluded), as displayed by thysanurans, all orthopteroid forms and the adults of neuropteroids, Mecoptera, Trichoptera, mandibulate zeuglopteran Lepidoptera and nonapoid Hymenoptera. The only group with fluid-feeding habits retaining five segments is the nematocerous Diptera, whose palps are not employed for food manipulation.

The second trend is formation of palps with additional segments--usually six or seven--among archaeognathans (Bitsch 1956) and apoid

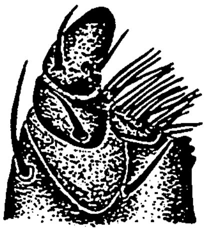
MAXILLARY PALPUS SEGMENTATION



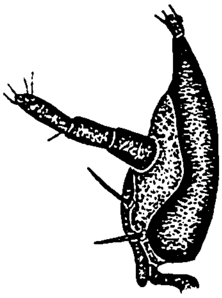
A. SEGMENTS ABSENT.
LEP: *Imma acosma* Turner.
Adult, [Philpott 1927].



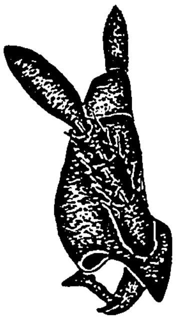
B. ONE SEGMENT.
TRI: *Sericosoma personatum* (Spence). Adult male, [Crichton 1957].



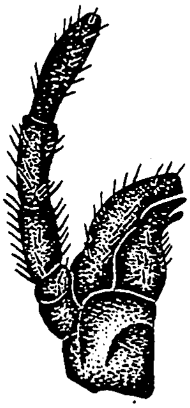
C. TWO SEGMENTS.
COL: *Peltodytes* sp.
Larva, [Jaboulet 1960].



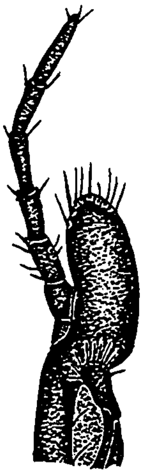
D. THREE SEGMENTS.
THY: *Chirothrips hamatus* (Trybom). Adult, [Jones 1954].



E. FOUR SEGMENTS.
SIP: *Ctenocephalus canis* (Curtis). Adult, [Wenk 1953].



F. FIVE SEGMENTS.
PHA: *Necrosia sparaxes* Westwood. Adult, [Gangrade 1965].



G. SIX OR MORE SEGMENTS.
HYM: *Hylaeus* sp.
Adult, [Saunders 1891].

FIGURE 19. Character-states of Character 35: maxillary palpus segmentation. Not drawn to scale.

hymenopterans (Michener 1944). According to Boudreaux (1987) the primitive number of maxillary palp segments is five, and forms with supernumerary segments have acquired them by secondary addition. However, Kukalovà-Peck (1987) concludes, based on recently described fossil material, that that maxillary palp segmentation is primitively eight. If so, virtually all extant insects have a reduced segment number. Among archaeognathans the palps are large, conspicuous and setate, and are probably used for tactile response and food manipulation. The palp shape resembles a primitive appendage (Sharov 1966) and in some related fossil forms appear to bear terminal tarsi (Kukalovà-Peck 1980) suggesting that seven or eight segments is the primitive number for insects (also indicated by Denis and Bitsch [1973] and Kukalovà-Peck 1987]). In the case of apoid hymenopterans, subdivision of the palp into six or seven segments is secondary (Crampton 1923b) and palps are probably used for food manipulation, akin to orthopteroid insects.

The third trend is reduction of maxillary segment number, of which there are several themes. One theme is reduction of segment number to four, evident in the adult Coleoptera (Williams 1938, Crowson 1981) and many adult Lepidoptera (Philoptt 1927), and also present in the Protura (Tuxen 1962), Psocoptera and Mallophaga (Symmons 1952) and Siphonaptera (Snodgrass 1946). Another theme is the presence of one to three maxillary segments among some aptery gotes (entotrophs and collembolans), paleopterans, thysanopterans, and adult brachyceran and cyclorrhaphan dipterans. A final theme is the occurrence of one to three segments among aquatic immatures of filter-feeding and carnivorous paleopterous naiads and dipteran and trichopteran larvae, as well as terrestrial coleopteran, lepidopteran and hymenopteran larvae (see Peterson 1948, 1950).

Lastly, the fourth trend is a consequence of maxillary reduction, namely the absence of maxillary palps. This trend characterizes (i) part of the *Baupläne* the fluid- feeding hemipteroid groups Anoplura, Homoptera and Heteroptera (partly from Parsons 1964b), (ii) various holometabolous larvae whereby maxillary supression or loss has occurred independently in numerous lineages (Bischoff 1922a, Ripley 1923, Clancy 1946) and (iii) in adult nectarivorous lepidopterans of the superfamily Papilionoidea (Philpott 1927).

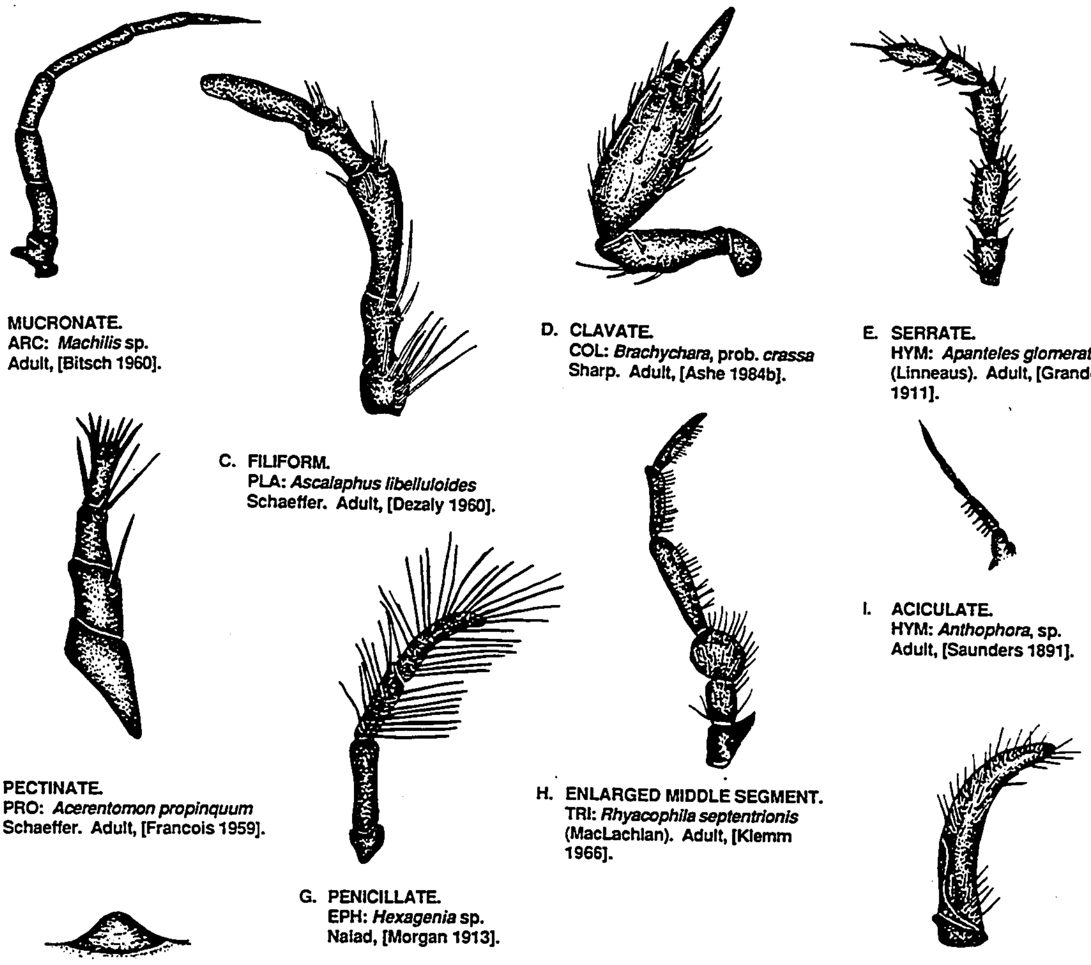
Although the patterns described above are coarse-grained trends that involve numerous taxonomically disparate groups which arose convergently, palp segment-number, on occasion, can vary intraspecifically. This has been demonstrated for castes belonging to many groups of ants (Kusnezov 1954a, 1954b) and it may be common in other social insects.

5.10.5. Maxillary Palpus Type (Character 36)

Three pairs of articulated appendages--maxillary palpi, labial palpi and antennae--are the major probing, sensory structures occurring on the heads of insects. Maxillary palpi are typical in this regard since they are instrumental in contacting, feeling and manipulating the food environment of the insect (Gangwere 1960, Chapman 1982; see Staedler 1977 for a review). The most generalized palpus type is filiform and occurs among solid food-feeding pterygotes (Fig. 20). Filiform palps are long, sensory, five-segmented, and associated with a full complement of maxillary appendages and usually a lobate galea. Filiform palps are provided with various sensory organs, including chemoreceptors in locusts (Thomas 1966, Chapman and Thomas 1978) and crickets (Klein and Müller 1978), sensory papillae in adult rove beetles (Blackwelder 1936) and pit sensillae in adult neuropterans (Chapman 1982). They serve a pivotal role in solid food selection (Blaney and Chapman 1970) and can assess food platability at significant distances from the head capsule (Roberts 1972). Filiform palps occur predominately in orthopteroids, adult neuropteroids, many adult panorpoids and most adult Hymenoptera. Morphological deviations from the generalized filiform condition include the serrate and clavate types. The serrate type is characterized by distal expansion and proximal narrowing of each palpal segment and is borne by solid food consumers such as mallophagans and adult coleopterans and hymenopterans. Clavate palpi possess pronounced distal expansion of the terminal segment and are found usually in adult solid-food-ingesting coleopterans.

Several other distinctive palp morphologies occur, associated with particular diets. Frequently palps become very hirsute and are employed in trapping fine particulate matter, particularly in the aquatic realm among brush-sweeping ephemeropteran naiads (Strenger 1954) and among nematocerous dipteran larvae (Pao and Knight 1970). In the terrestrial realm, adult fluid-feeding lepidopterans have converted hairs to a dense vestiture of shingled scales on a tactile palp that has been reduced in size and segment number (Walter 1885a). This reduction presumably is a

MAXILLARY PALPUS TYPE



B. MUCRONATE.
ARC: *Machilis* sp.
Adult, [Bitsch 1960].

C. FILIFORM.
PLA: *Ascalaphus libelluloides*
Schaeffer. Adult, [Dezaly 1960].

D. CLAVATE.
COL: *Brachychara*, prob. *crassa*
Sharp. Adult, [Ashe 1984b].

E. SERRATE.
HYM: *Apanteles glomeratus*
(Linneaus). Adult, [Grandori
1911].

F. PECTINATE.
PRO: *Acerentomon propinquum*
Schaeffer. Adult, [Francois 1959].

G. PENICILLATE.
EPH: *Hexagenia* sp.
Naiad, [Morgan 1913].

H. ENLARGED MIDDLE SEGMENT.
TRI: *Rhyacophila septentrionis*
(MacLachlan). Adult, [Klemm
1966].

I. ACICULATE.
HYM: *Anthophora*, sp.
Adult, [Saunders 1891].

J. PAPILLATE.
HYM: *Anthophora sanfordiana*
Cockerell. Larva, [Michener 1953].

K. APPRESSED LOBE.
ODO: *Onchyogomphus ardens*
Needham. Adult, [Chan 1953].

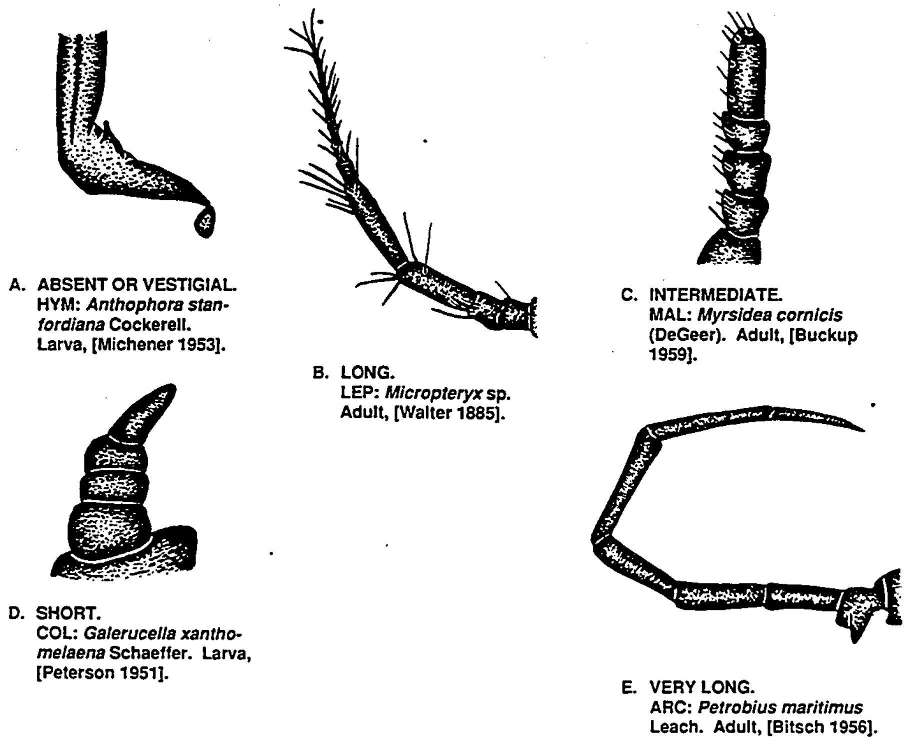
FIGURE 20. Character-states of Character 36: maxillary palpus type. Not drawn to scale.

response to enlargement of the long, hairy proboscis, which has assumed much of the mechanoreceptive function (Philpott 1927). Notably, maxillary palps, unlike galeae and laciniae, are not used as brush-sweeping organs in floricolous beetles (Grinfel'd 1975, Crowson 1981). In some adult Coleoptera, such as the Paussidae and in some adult Trichoptera, an enlarged middle segment indicates expansion of a specialized sensory organ (Cummings 1913, 1914; Crichton 1957). A unique condition exists among insectivorous odonatan adults, wherein the maxillary palp is a short lobe appressed to a raptorial mala (Hakim 1964). Larval maxillary palpi are generally diminutive and usually are either setigerous or aciculate, as in herbivorous lepidopterans or hymenopterans (Dethier 1937, Jayewickreme 1940, Lorenz and Kraus 1957), or short and stubby in ominivorous to carnivorous coleopterans, dipterans and trichopterans (Lloyd and Lloyd 1921, Dethier 1937, Teskey 1976).

5.10.6. Maxillary Palpus Aspect-Ratio (Character 37)

Maxillary palpus aspect-ratio is determined by the ratio of average segment width to total palpus length, excluding setae and the palpiger but including terminal organs such as the palpal cone. The total range of palpal aspect-ratio can extend from an inconspicuous protuberance on the maxillary main-body in many larvae (Peterson 1948, 1951) to prominent, gracile appendages several times the antennal length in adult hydrophilid beetles (Golden 1925). (See Crampton [1923b] for a synoptic study.) (Fig. 21). Most maxillary palpi are long or, less

MAXILLARY PALPUS ASPECT RATIO



A. ABSENT OR VESTIGIAL.
HYM: *Anthophora stanfordiana* Cockerell.
Larva, [Michener 1953].

B. LONG.
LEP: *Micropteryx* sp.
Adult, [Walter 1885].

C. INTERMEDIATE.
MAL: *Myrsidea cornicis* (DeGeer). Adult, [Buckup 1959].

D. SHORT.
COL: *Galerucella xanthomelaena* Schaeffer. Larva, [Peterson 1951].

E. VERY LONG.
ARC: *Petrobius maritimus* Leach. Adult, [Bitsch 1956].

FIGURE 21. Character-states of Character 37: maxillary palpus aspect-ratio. Not drawn to scale.

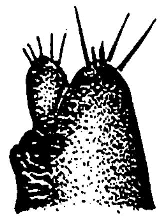
commonly, intermediate in length. Long maxillary palpi are strongly associated with archaeognathan and thysanuran apterygotes and especially with the orthopteroid and adult neuropteroid assemblages but subordinately with the panorpoids. In virtually all of these groups, palpi are used for sensing and manipulating solid or particulate food (see Yuasa [1920], Philpott [1927] and Williams [1938] for examples). Very long palpi principally occur among omnivorous or necrovorous psocopterans (Weber 1938b), especially the Raphidophoridae (Richards 1955, Wada 1965) and the Gryllidae (Golden 1925) among orthopterans, where the palpi generally are invested with various types of chemical and tactile sensillae (Klein and Müller 1978). Additionally, very long palpi occur sporadically among adult carnivorous coleopterans and typically are involved in the subduing of live prey (Schmitz 1943, Cook 1943); they also occur in specialized forms such as the lepidopteran Micropterygidae, which uses its long, acuminate palp as a "pollen scratcher" for extracting pollen from flowers (Barth 1985).

Palpi of intermediate and short aspect-ratio are fairly diagnostic of anthophilous forms, such as the Thysanoptera and especially certain coleopteran adults, where they are often clavate and bear special terminal setation used in securing pollen or spores (Pradhan 1939, Grinfel'd 1975). Also, the largely lignivorous Isoptera and many nectarivorous Lepidoptera possess intermediate-length maxillary palpi. By contrast, forms with small, stubby palpi are predominantly holometabolous larval forms which characteristically bear abbreviated cephalic appendages and well-developed mandibles. Adult forms with short or vestigial maxillary palpi are usually those groups that have prolonged or otherwise expanded fluid-feeding organs such as the labellum of cyclorrhaphan Diptera (Peterson 1916), the galeal siphon of ditrysian Lepidoptera (Walter 1885, Philpott 1927) and the maxillolabial complex of some apoid hymenopterans, including the Megachilidae and Apidae (Saunders 1891). Wesché (1904) has presented, for muscoid flies, a morphological transition series in which decreasing palpal length is correlated with increasing labellar length, increasing ligular development and decreasing eye pubescence.

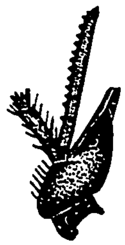
5.10.7. Galeal Modifications
(Character 38)

With the exception of the mandibles, the galea and lacinia constitute the most diagnostic mouthpart elements in insects. Galeal and lacinial form is associated with the trophic role of various insect groups, and in numerous instances similar modes of individual element development and multielement co-optation have arisen independently. The general function of the galea in solid-feeding orthopteroid and neuropteroid insects is to serve as a tonguelike lobe for the forwardly-directed shoving of food into the cibarium (Gangwere 1960, 1966; Smith 1985). In more derived forms the galea has been modified into three general modes. One mode is the elaboration of hairs and/or sclerification, changing a modestly setate, lingulate lobe into structures such as a penicillate brush, a pectinate sieve or rake, an acessory pair of "mandibles" or subsegmented palpiform prolongations (Fig. 22). In such forms the galeae and laciniae remain separate elements and the galea is modified principally in vestiture and dermal processes but not dramatically in fundamental shape. The second mode of modification is a marked

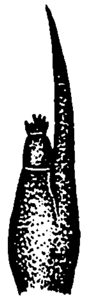
GALEAL MODIFICATIONS



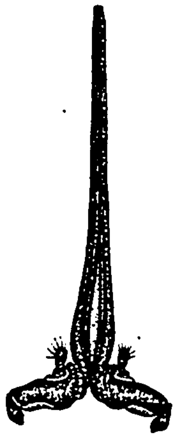
B GENERALIZED.
DPL: *Campodea chardardi* Conde. Adult, [Francois 1970].



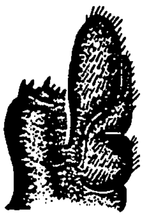
C. CONJOINED LEVER.
SIP: *Ctenocephalides felis* (Bouche). Adult, [Snodgrass 1946].



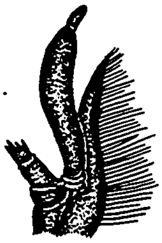
D. STYLATE.
PRO: *Acerentomon affine* (Bagnold). Adult, [Francois 1969].



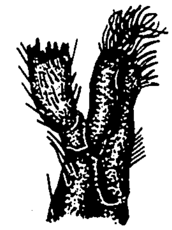
E. SIPHONATE.
LEP: *Synanthedon exitosa* (Say). Adult, [Snodgrass 1935].



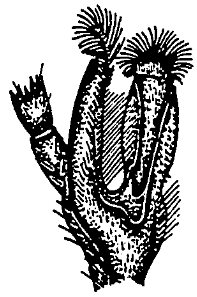
F. LINGULATE.
MEC: *Panorpa communis* Linneaus. Larva, [Bierbrodt 1943].



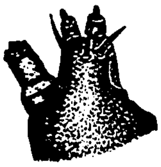
G. PALPIFORM.
PLA: *Myrmeleon europaeus* Linneaus. Adult, [Korn 1943].



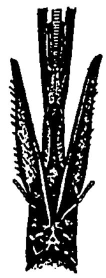
H. PENICILLATE.
COL: *Eucinetus meridionalis* Castineau. Adult, [Vit 1977].



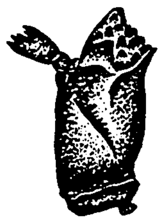
I. PECTINATE.
MEC: *Panorpa communis* Linneaus. Adult, [Heddergott 1938].



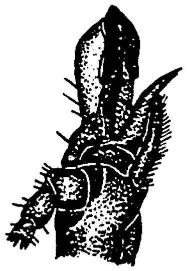
J. LOBATE, WITH SENSILLAE.
LEP: *Coleophora veroniella* Chambers. Larva, [DeGryse 1915].



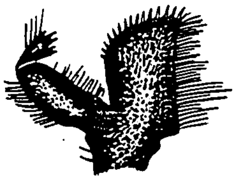
K. AMPLEXIFORM/ LAMELLATE.
HYM: *Anthophora* sp. Adult, [Saunders 1891].



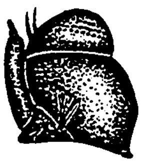
L. MANDIBULATE.
COL: *Melolontha vulgaris* Fabricius. Adult, [Osterwald 1954].



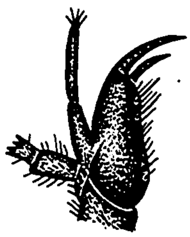
M. VAGINATE.
BLA: *Periplaneta americana* (Linneaus). Adult, [Bugnion 1920].



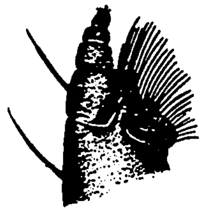
N. CONJOINED, COMB AND RAKE.
EPH: *Heptagenia*, sp. Adult, [Spieth 1933].



O. CONJOINED, GENERALIZED.
DIP: *Armigeres malayi* Theobald. Larva, [Cook 1944b].



P. ELONGATE + TERMINAL SETAE/SPINES.
PLE: *Acroneuria abnormis* Newman. Naiad, [Claassen 1931].



Q. CONJOINED, PENICILLATE.
COL: *Cionus scrophulariae* Linneaus. Adult, [Donges 1954].

FIGURE 22. Character-states of Character 38: galeal modifications. Not drawn to scale.

elaboration of form, with or without a concomitant co-optation of intramaxillary or extramaxillary elements. This mode includes galeal structures such as siphons, stylets, or participation in the wall formation of an oral cone. The third mode involves coalescense with the lacinia to form mostly a generalized mala in holometabolous larvae or, less commonly, more specialized fimbriate, pectinate or rakelike structures. These latter morphologies are often functionally convergent with the first mode.

The generalized and unmodified galea consists of a fleshy, robust, sparsely to moderately setate lobe used for sensory monitoring (Thomas 1966, Roberts 1972) and handling (Bertin 1923, Gangwere 1960) of food. Generalized galeae principally are present in apterygotes (Protura excepted), the Embioptera, adult Planipennia and sporadically among larvae of many major holometabolous orders. A somewhat more modified condition is a gracile, lingulate lobe, also found in solid-food consumers--in members belonging to groups as disparate as orthopterans, mallophagans, raphidiopterans, trichopterans, larval ditrysian lepidopterans and larval symphytan hymenopterans (see Crampton 1923b for some examples). Among some orthopteroids, particularly blattoids, mantodeans, phasmatodeans and isopterans, the galea is hood-shaped, presumably serving as a lacinial "cover" (Yuasa 1920, Roberts 1972). Another modification of the generalized condition is a palpiform, "segmented" galea, which is commonly characterized by a pseudoarticulation separating a basigaleal "segment" from a distigalea (Crampton 1923b, Crowson 1981). Palpiform galeae are elongate and are moderately diverse morphologically (though not as diverse as maxillary or labial palps) and can range from aciculate picks in plecopteran naiads (Crampton 1923b), to typical palpal appendages in carnivorous cicindelids (Evans 1965b), carabids (Golden 1925) and cocinellids (Pradhan 1938, Butt 1951), to fimbriate "featherdusters" among floricolous beetles such as the Rhipiphoridae and Mordellidae (Crowson 1981). In a few carnivorous groups galeae are transformed into mandiblelike forms, usually in conjunction with laciniae (although it is the laciniae that are more often transformed into mandibles, e.g. Adams and Salamon [1972]). Although mandiblelike galeae bear teeth and often serve as a second pair of jaws, they have been documented mostly in folivorous scarabaeids (Bertin 1923, Golden 1925) and several trichopteran adults that have rudimentary mandibles (Crichton 1957).

One of the more notable deviations from the generalized lobe has involved elaboration of hair, coarse setae, or spines to carry out the functions of sweeping, raking and filtering. This first mode of galeal modification is deployed into two broad characterizations: various fimbriate or penicillate galeae found predominantly in terrestrial adults and several pectinate modifications occurring mostly in immature aquatic forms. In the terrestrial realm, penicillate galeae--characterized by development of terminal tufts or brushes of hairs--is a recurring theme among floricolous and fungicolous forms, especially in adult and some larval beetles (see Barth [1985] and Ashe [1984a, 1984b], respectively). Among floricolous forms, galeae were described as "*touffles au pinceaux*" (Bertin 1923: 153) and "*reichlich mit langen Borsten besetzt*" (Golden 1925: 45) for pollenivorous Scarabaeidae. Blackwelder (1936: 16) later described galeae as similar to a "densely hairy lobe" in the Staphylinidae and Evans (1965b: 47) examined a brushlike galea "used to hold the food and push it dorsally" in an insectivorous genus of Carabidae. Even more elaborate mechanisms have been described for pollinivory in Melyridae (Schicha 1967, Barth 1985) and Mordellidae (Fuchs 1974) and for the Oedemeridae and Coccinellidae (Grinfel'd 1975). These studies document the galea as an important component of a multielement ensemble of mouthparts, each which is invested with appropriately positioned brushes and adhesive hair glands to sweep, collect and transport pollen particles from stamens into the cibarium. Good general accounts of mouthpart morphology and function among pollinivores can be found in Schicha (1967), Fuchs (1974), Grinfel'd (1975) and Barth (1985).

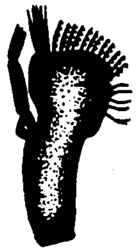
In the aquatic realm, galeae, like other mouthpart elements, have been altered to function as various pectinate filtering or raking devices. This is particularly evident among stratiomyiid dipteran larvae filtering suspended particulate detritus (Vaillant and Delhom 1956). More commonly, the galea has been fused with the lacinia, producing a mala bearing either (i) finely meshed setal fans used for filtering, (ii) coarsely spaced spines used for raking benthic detritus or scraping surface films on on substrates, or (iii) some combination of both structures (see Cummins and Merritt 1984). (This is the third mode of galeal modification.) Malar filtering fans occur especially among many ephemeropteran and dipteran larvae, where active filtration is accomplished either by oral-based particle trapping and sucking processes (Brown 1961), or by the construction of a tubular burrow and the use of various appendages to generate a water current for active interception of seston in a cephalic sieve (Walshe 1951, Hardland-Rowe 1953). Rakelike malar pectines occur in some ephemeropteran naiads, a few coleopteran larvae and many dipteran larvae, where they are used for actively gathering benthic particulate matter and substrate-attached films (Cummins and Merritt 1984, Teskey 1984). In odonatan naiads, malar spines are used for recapturing food droppings from the oral chamber and returning it to the mouth (Pritchard 1976).

Profound modifications of the galea, in association with major morphological realignments with other mouthpart elements, characterize the second mode of galeal modification. In the Protura and among a few families of Coleoptera, especially the Rhysodidae and Cerylonidae, the stilleto-shaped galeae are major stylate elements for the piercing of fungal hyphae (Sturm 1959, Francois 1969, Besuchet 1972, Crowson 1981, respectively). In the Siphonaptera, the galea is transformed into a "lever" that, when pushed posteriorly, engages the lacinial stylet for downward protraction (Snodgrass 1944). Probably the most spectacular modification is the conjoining of both galeae medially to form an elongate, protrusible and recoilable siphon that has a cross-section approximating an open figure-8 with a median tube (Eastham and Eassa 1955). This structure is used by fluid- and semi-fluid feeders and has originated at least four times: in nonzeuglopteran Lepidoptera (Schmitt 1930), Dipseudopsidae of the Trichoptera (Ulmer 1905), and Meloidae (Smith 1898) and Rhipiphoridae (suggested by Williams 1938) of the Coleoptera. Although the galeae are similarly elongated in many glossa-bearing, apoid Hymenoptera, they however consist of separate, articulating elements that are U-shaped in cross-section and serve as glossal clamps to squeeze fluid from a retracting glossa (Snodgrass 1956, Winston 1979). In some specialized haustellate groups such as the Thysanoptera, the galea is fused with other mouthpart elements and contributes to the formation of the mouthcone (Peterson 1915).

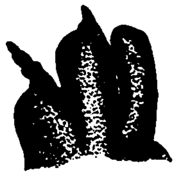
The last mode of modification--galeolacinial fusion into a mala--was mentioned above in connection with various pectinate fans and rakes. A stumpy, generalized malar lobe occurs, however, in many terrestrial holometabolous larvae, in association with reduction of other cephalic appendages. In many holometabolous larval forms, the malar lobe is entirely lacking, due either to local supression of only the galeal region (Planipennia and Trichoptera) or complete absence of the maxilla (Diptera and Hymenoptera) (after Snodgrass 1935).

5.10.8. Lacinial Modifications (Character 38)

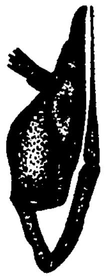
Like the galea, the lacinia is variously modified into several structural and functional types (Fig. 23). The scope of modification ranges from the generalized condition, to palpiform and mandible-like structures, to diverse penicillate and pectinate processes and culminates in stylets of various length and dentition. Additionally, the lacinia often is fused to the galea in many groups, forming a composite structure in paleopterous naiads and some holometabolous larvae. For pterygotes, the generalized lacinial condition consists of a sclerotized, mesially-directed, falcate structure with a row (or rows) of spines, usually surmounted by a larger, distal spine. Such a structure



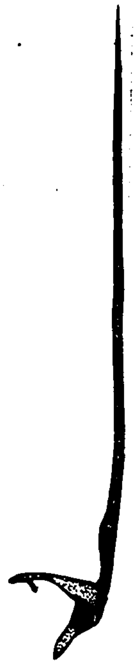
B GENERALIZED.
EPH: *Ameletus inopinatus* Eaton. Naiad, [Landa 1969].



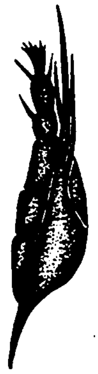
C. LINGULATE.
HYM: *Sirex cyaneus* Fabricius. Larva, [Short 1952].



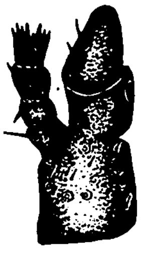
D. STYLATE, SHORT.
THY: *Heliothrips*, sp. Adult, [Crampton 1923b].



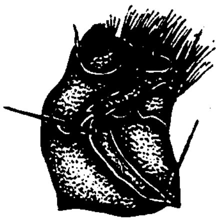
E. STYLATE, LONG.
HOM: *Magicicada septendecim* Linneaus. Adult, [Kramer 1950].



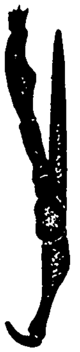
F. DISTYLATE.
PRO: *Acerentomon propinquum* (Conde). Adult, [Francois 1959].



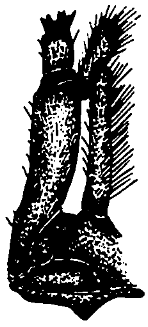
G. GENERALIZED-MALA.
RAP: *Raphidia notata* Fabricius. Larva, [Genay 1953].



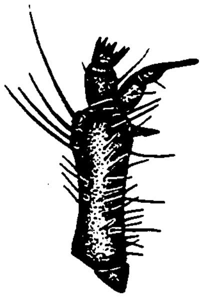
H. FIMBRIATE MALA.
DIP: *Tipula livida* Van der Wulp. Larva, ventral aspect, [Chiswell 1955].



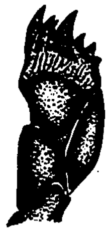
I. ELONGATE-FLESHY.
MEC: *Nannochorista dipteroides* Tillyard. Adult, ventral aspect, [Hoyt 1952].



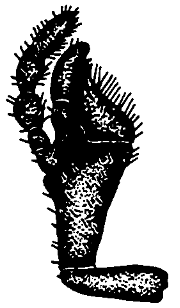
J. PENICILLATE.
COL: *Leptopalpus rostratus* Fabricius. Adult, [Handschin 1929].



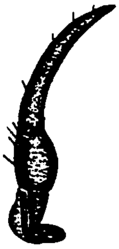
K. SPINOSE.
COL: *Loricera*, sp. Larva, [Richards & Davies 1977].



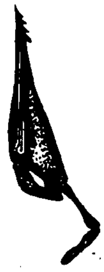
L. MANDIBULATE.
COM: *Brachystomella parvula* (Schaeffer). Adult, [Adams & Salamon 1972].



M. PECTINATE-SPINOSE.
ISO: *Kalotermes flavicollis* Fabricius. Adult, ventral view, [Richard 1951].

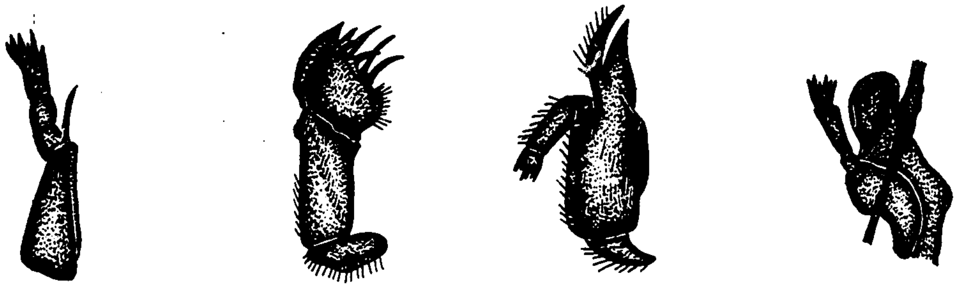


N. FALCATE-GROOVED.
PLA: *Chrysopa viridiana* Schneider. Larva, ventral view, [Principi 1959].



O. STYLATE-GROOVED.
PLA: *Semidalis aleuriformis* Stephens. Larva, dorsal view, [Rousset 1966].

LACINIAL MODIFICATIONS (CONTINUED)



P. ACICULATE.
DIP: *Liriope lenis* (Osten Sachen). Adult, [Hoyt 1952]

Q SPINOSE/SETATE MALA.
ODO: *Aeshna juncea* (Linneaus). Adult, [Popham & Bevons 1979].

R. MUCRONATE. .
PLE: *Alloperla minuta* Banks. Adult, ventral view, [Hoke 1924].

S. MAXILLARY PICK.
PSO: *Psocus confraternus* Banks. Adult, [Cope 1940].

FIGURE 23. Character-states of Character 39: lacinial modifications Not drawn to scale.

provides a mechanical role of manipulating food before mandibular comminution (Gangwere 1960, 1966) as well as a gustatory function through the detection of food quality by chemosensillae and mechanosensillae (Thomas 1966). This basic structure (and minor modifications of it) is present in virtually all orthopteroids, many adult neuropteroids and sporadically among larval Trichoptera and Hymenoptera. With the wide breadth of diets possessed by groups bearing the generalized condition, the only meaningful, diet-related characterization is that such laciniae are associated with solid-food ingestion. Major modification of the generalized lacinia has taken several major directions. These directions include transformations into (i) galea-like, spatulate lobes among some adult lepidopterans and hymenopterans (Tillyard 1923b; Stephen et al. 1969), (ii) nonlinguloid, robust projections among larvae of the same groups (Lorenz and Kraus 1957), (iii) a palpiform structure in adult dipterans (Hoyt 1952), or (iv) a sclerified, dentate, jaw-like structure among collembolans (Goto 1972) and some omnivorous orthopterans (Golden 1925). The lacinia also bears several structures that have structural parallels in the galea, including fimbriate brushes that especially occur among adult coleopteran, mecopteran and aculeate hymenopteran species (Ashe 1984b; Otanes 1922; and Bugnion 1919, 1929, 1930, respectively).

A penicillate lacinia is often significantly different from the adjacent penicillate galea on the same maxilla. Frequently the vestiture on both lobes varies in density, placement, hair or setal length, and hair or setal coarseness (e.g. see Ashe 1984b). Often the lacinia and galea, as separate elements, provide different functions for the capture and transport of the same food (Barth 1985). For example, in pollenivorous forms the galeal lobe specializes in capturing pollen and the lacinia is involved in the transportation of pollen forward to the mouth (Schicha 1967). In other forms the lacinia and galea are fused, forming a penicillate mala with uniform setation. In general, penicillate laciniae have been associated with pollenivory in anthophilous forms and sporivory in mycophilous forms (e.g. the "pollen broom" of Barth [1985] and the "spore brush" of Ashe [1984b], respectively).

A pectinate lacinia or mala is found, for different reasons, in aquatic immature forms and in terrestrial adult forms. Among aquatic forms, a pectinate lacinia is found in paleopteran naiads, where they are fused with the galeae to form rake-like malar structures for collecting particulate debris in ephemeropterans (Froelich 1964), or spinose processes for trapping food fragments exiting the cibarium in carnivorous odonatans (Pritchard 1976; see Section 5.10.7). For aquatic nematocerous dipterans, pectinate malae are elements constituting the cephalic filtration fan in various lacustrine and riverine species (Embden 1932; Gouin 1957, 1959; Kennedy 1958). In terrestrial forms, especially larval coleopterans, spinose and setate malae are used for securing and transporting particulate food, mainly spores and pollen among Erotylidae, Endomychidae, Mycetophagidae, Colydidae, and other principally cucujoid families (Crowson 1981). Spinose and setate malae are also used for handling macerated food (often insect) fragments in the Staphylinidae, Cleroidea, Tenebrionidae, Chrysomelidae and Curculionoidea (see Bitsch 1966, Crowson 1981).

The most notable lacinial modification is the presence of various tissue-piercing, styliform structures in several insect groups. Among haustellum-bearing forms, lacinial stylets are almost always associated with galeal absence (Matsuda 1965); among nonhaustellate groups, lacinial stylets are often shorter and have associated galeal stylets (Francois 1969, Dajoz 1976, Vit 1977). Lacinial stylets have independently arose at least 14 times, namely in the Protura, Collembola (Neauridae), Orthoptera (Cooloolidae), Mallophaga (Haematomyzidae), Homoptera/Heteroptera, Thysanoptera, Coleoptera (Sphaeriidae, Rhysodidae, Leioidae, Eucinetidae, Cerylonidae, Corylophidae), Siphonaptera (see Matsuda 1965) and Diptera. Notably, stylate laciniae and associated mouthpart structures have originated minimally four times within the Coleoptera (Crowson 1981, Pakaluk 1987). In some groups, lacinial stylets work in coordina tion with paired mandibular stylets, as is the case for the Protura, Homoptera/Heteroptera, coleopteran Cerylonidae and Diptera. In one group, thysanopterans, lacinial stylets work in conjunction with a single, unpaired mandible. In other groups, lacinial stylets are not associated with mandibles, as exeplified by the collembolan Neanuridae, orthopteran Cooloolidae, coleopteran Sphaeriidae, Rhysodidae and Eucinetidae, and Siphonaptera--often in combination with an epipharyngeal or hypopharyngeal stylet. Lacinial stylets are generally long and slender in haustellate deep tissue-feeding groups, such as sanguinivorous heteropterans and dipterans (Barth 1953, Downes 1971); they are frequently relatively short among nonhaustellate, shallow tissue-feeding groups, including thysanopterans (Doeksen 1941) and various coleopteran species that pierce-and-suck fungal filaments

(Crowson 1981). Like mandibular stylets, lacinial stylets can be edentate or bear distal barbs, ridges, or serrations to facilitate cutting or slicing through tissue (Cobben 1978).

A morphologically related but functionally unique structure, consisting of a long, sclerotized rod with a blunt, scalloped terminus, is the "maxillary pick" of psocopterans and some mallophagans (Cope 1940). Although the function of the pick is incompletely understood, the maxillary pick in psocopterans may be used used as a support prop during feeding (Pearman 1928) or as a pick or chisel (Burgess 1878, Denis and Bitsch 1973), possibly to extract food. It appears that the pick can be protracted and retracted in a manner similar to a stylet (Matsuda 1965). A second, major type of lacinial structure used for piercing-and-sucking occurs in obligately insectivorous, larval Planipennia. The lacinia or (according to some) a stipital extension (Korn 1943) is used as a falcate, acuminate stylet that bears two longitudinal grooves on its ventral surface.

These two grooves exactly match two dorsal grooves on the similarly falcate dorsal mandibular stylet (Matsuda 1965). When both stylets are placed in direct apposition for concerted adduction, one of the resultant canals is used for outgoing venom for immobilizing and liquefying prey, while the other, wider canal serves for transport of incoming fluid food (Wundt 1961). Piercing in most planipennian larvae is achieved by coordinated clamping of the mandible/lacinial stylet apparatus on prey items (Lozinski 1908, Rousset 1956, Griffiths 1980). In some sponge-consuming aquatic forms, the mandible/lacinial apparatus is linear rather than falcate and is probably characterized by protraction and retraction (Withycombe 1924).

Lacinial absence mirrors galeal absence in that there are two basic ways that it is deployed. One way is complete or near-complete suppression in specialized or nonfeeding groups such as anoplurans, male coccoid homopterans and virtually all strepsipterans. The other way is occasional supression of the maxilla, especially the mala and palpi, in various isolated forms among holometabolous larvae.

5.10.9. Participation of the Maxilla in a Multielement Mouthpart Structure (Character 40)

Three major trends of multielement co-optation characterize the maxilla. These are (i) formation of stylets in various piercing-and-sucking groups, (ii) varied structures for the siphoning, sponging and lapping of surface fluids and (iii) contribution as a sclerite to a rostral wall in some biting-and-chewing forms. When all three trends are assessed, it is evident that the maxilla, or particular maxillary elements, have been overwhelmingly co-opted into liquid-feeding structures rather than into new rearrangements of a basically solid-feeding apparatus.

The formation of multielement complexes involving stylets has occurred haustellate and nonhaustellate groups. In most major haustellum bearing groups--hemipteroids and dipterans in particular--the maxilla has provided a pair of lacinial stylets that are often in apposition with a mandibular stylet pair, the ensemble of which is ensheathed by a labium (Smith 1985). Among haustellum-lacking forms, lacinial and less commonly galeal, stylets are often co-ordinated with a mandibular stylet pair, with no or minimal labial participation (Dajoz 1976). Larval planipennians are similarly nonhaustellate but achieve piercing by overlaying a maxillary extension--probably the lacinia--on a falcate mandible to produce a resulting tubular structure for sucking fluids in the adducted state (Wundt 1961).

Varied styles of surface fluid-feeding exist in insects, virtually all which involve major modifications of the maxilla and labium, either separately or conjointly. The maxillary siphon of lepidopterans, coleopterans and a few other groups is principally an intramaxillary multielement complex, although it bears few structural contributions from adjacent mouthpart regions. In lepidopterans, the maxillary siphon is associated with mandibular and glossal/paraglossal absence or reduction as a structural concomitant (Mosher 1915). Insects producing distally flared, fleshy structures that are ventrally deployed in active or passive sponging of surface fluids include the hypopharynx of gryllid orthopterans (Rietschel 1953), the haustorium of adult trichopterans (Cummings 1914) and the labellum of adult cyclorrhaphan dipterans (Peterson 1916). These three structures include some interacting maxillary elements, although the haustorium is dominately hypopharyngeal and the labellum is mostly labial in origin. The maxillolabial complex in nonapoid aculeate hymenopterans functions as a single unit for solid-food feeding. However, in apoid forms it is characterized by glossal elongation for lapping and transformation of the galeal and palpal structures for squeezing fluids trapped in the densely hirsute glossae (Snodgrass 1942).

Among more recognizably "mandibulate" forms, the maxillary main-body is part of the adult snout wall in curculionid coleopterans, mecopterans and nemopterid planipennians. Among coleopterans, mandibles, palps and other lobes are apically located (Dönges 1954), serving as part of a "drilling" armature for boring into hardened foods. Among mecopterans, movable mouthpart elements are prolonged and more basally attached. In passing, it should be noted that a vast assemblage of paleopteran adults, orthopteroids, most adult neuropterids and some hymenopterans--at least half of the species examined--lack any multi-element co-optation.

5.11. Character-Group IX: Labial Region

The labium bears elements analogous and homologous to the maxilla (Snodgrass 1935), including a pair of lateral palpi and two pairs of medial lobes: the outer paraglossae and the inner glossae. However, unlike the maxilla, the labium is a mesially unpaired structure, even though it bears lateral paired appendages. In contrast with the mandibles and maxillae, the presence of a central area of unpaired sclerites--the submentum/mentum/prementum series--has allowed for structural fusion to other unpaired mouthpart regions, especially the labrum and hypopharynx. In addition, fusion of labial appendages themselves, particularly the palpi, have broadened the range of labial participation in multielement structures. These two reasons--(i) the presence of a series of ectal, mesial sclerites that are intimately co-opted by other regions to produce composite structures and (ii) the existence of paired labial appendages that form structures to house mouthpart elements from other regions--are the principal reasons for the success of the labium in multielement mouthpart co-optation. Five major structural trends characterize the spectrum of labium development in insects. First is the primitively specialized condition of the formation of a gnathal pouch, contributing to entognathy in apterygotes (Manton 1977); and second, for ectognathous insects, a generalized complete labium with a postmentum (submentum + mentum) and three pairs of appendages: palpi, paraglossae and glossae (Walker 1931a). This latter generalized condition occurs in the more derived apterygotes--archaeognathans and thysanurans, as well as in adult paleopterans, orthopteroids, psocopterans, mallophagans, most coleopterans and many hymenopterans (Crampton 1928, Walker 1931b; see also Williams [1938] for examples without textual comment). Among such groups the labium functions as a "lower lip," complementing the labrum, or "upper lip" (Snodgrass 1935). The second trend consists of the frequent occurrence of major structural reduction or even complete absence of the labium in holometabolous larvae (Anderson 1936, Das 1938, Jayewickreme 1940, Badcock 1961). Structural reduction includes decreases in palpal segment number and size, fusion or dimunition of glossae, supression of paraglossae and decrease in differentiation of the axial, labial sclerites. The third and fourth trends involve different routes toward the acquisition of fluid food: namely (i) piercing for fluid in unexposed shallow or deep tissue, and (ii) various feeding mechanisms for extracting exposed surface fluids. Piercing is accomplished with or without the use of a haustellum. Haustella originated by two major, distinct ways: first by prolongation and subsegmentation of axial labial sclerites which envelop similarly elongated maxillary and mandibular stylets in hemipteroids (Cobben 1978, Hamilton 1981); and second by labial palpal fusion around various mandibular, maxillary, hypopharyngeal and labral/epipharyngeal stylets in dipterans (Imms 1944, Hoyt 1952) and siphonapterans (Wenk 1953, Matsuda 1965). These haustella and other structures range from segmented, articulatory structures to nonsegmented sheaths for housing up to six stylets, to nonenveloping structures that provide guides for stylets in proturans and some coleopterans (Francois 1969, Besuchet 1972). Third, the labium and adjacent mouthpart regions are co-opted into an assortment of feeding organs involved in the uptake of surface fluids in adult holometabolous insects. These feeding mechanisms and multielement mouthpart structures include the glossate complex that is characterized by lapping-and-squeezing in predominately nectarivorous apoid hymenopterans (the labiomaxillary complex of Winston [1979]), and various, ventral, fleshy expansions used for sponging fluids such as the labellum of many cyclorrhaphan dipterans (Kraepelin 1883, Dethier 1959) and the "haustorium" of trichopterans (Crichton 1957).

Last, there is a varied assemblage representing an alteration of basic mandibulate mouthparts for specialization on unconventional diets or for unique feeding strategies. Such multielement structures departing from typical biting-and-chewing forms are the elongate rostra, with drill-like terminal mouthparts of dominately durophagous curculio noid coleopterans (Crowson 1981) and the elongate, hypognathous, suctorial rostrum of generally necrovorous mecopterans (Otanes 1922). Two structures that permit unique feeding strategies are the raptorial sling possessed by larval odonatans (Snodgrass 1954) and an adult coleopteran, *Stenus* (Weinreich 1968); and the protrusible labiohypopharyngeal spinneret of larval trichopterans, lepidopterans and symphytan hymenopterans (Crampton 1921b), which in some is employed as a net for trapping particulate food (Wallace and Malas 1976) and for others is used for constructing dwellings (Jayewickreme 1940).

From this wealth of structural variation, it appears that the labial palps are the most important single source of multielement cooptation. Predominately through fusion, the labial palps have independently given rise to stylet-ensheathing haustella in the hemipteroids, dipterans, siphonapterans and several other less diverse groups. The postmentum, prementum and their subsidiary sclerites are also important labial structures in interregion fusion, since they are major contributors to the "haustorium" of adult trichopterans and the spinneret of some larval holometabolans. The glossae are instrumental only in the lapping "tongue" of apoid hymenopterans, whereas the paraglossae are almost always absent in holometabolous insects (Crampton 1925a, Matsuda 1965) and are not an important part of a multielement structural innovation in any known group.

5.11.1. General Shape of the Labial Main-Body (Character 41)

Labial shape is an approximate indicator of the basic type and general position of mouthparts. This arises because, when mouthparts are placed anteriorly or inferiorly on the head capsule, the gular and labial sclerites must accordingly be prolonged or shortened, respectively, for accomodation of the positional change (see Section 4.3.4, or

Anderson [1936] and DuPorte [1957] for an analogous argument concerning gular elongation). Groups lacking a main-body also lack a labium, do not feed through the use of mouthparts and are almost always parasitic. (Notably, many free-living, nonfeeding, ephemeral adults have rudimentary mouthparts.) Alabiate groups include adult coccoid homopterans, adult neotenic strepsipterans and chalcidoid and proctotrupoid larval hymenopterans, all of which are endoparasitic or exoparasitic and feed either by cutaneous assimilation (Kinzelbach 1966) or by ingestion with structures resembling mouthhooks (Thorpe 1941). Other alabiate forms occur sporadically among larval dipterans of diverse diets and are also characterized by pronounced maxillary reduction.

A transversely elongate labial main-body is a consequence of a beak, proboscis or sometimes a rostrum whose base is broadly attached to the anterior or inferior aspect of the cephalic capsule. Consequently, forms bearing such a transversely-expanded labial sclerite are those feeding on liquids. By contrast, groups with an equant or elongate main-body are both solid- and liquid-feeders and apparently indistinguishably intergrade with each other. However, it appears that elongate main-bodies are, as a group, possessed by prognathous forms, particularly apterygote, paleopteran, orthopteroid and some larval and adult neuroptoid forms (Crampton 1923a, Walker 1931a), whereas equant main bodies occur in some neuropteroids and principally in liquid-feeding adult and larval panorpoids. Very elongated main bodies characterize either hypognathous, proboscate mouthparts, in the case of adult mecopterans and dipterans (Crampton 1925a) and adult cerambycid coleopterans, or a lateral narrowing of the labial mental area in some orthopteroids (Walker 1931a) and in larval symphytan hymenopterans. No specific feeding style or diet apparently is associated with a very elongate main-body.

5.11.2. Labial Main-Body Segmentation (Character 42)

Segmentation of the labial main-body is characterized by three general patterns: (i) a primitive condition of two segments, (ii) segment increase to three segments and (iii) a segment decrease to one segment, culminating in labial absence. The generalized labial condition consists of two sclerites--a proximal postlabium and a distal prelabium (Snodgrass 1935)--and is found in apterygotes, paleopterans, nonbeaked hemipteroids, some neuropteroids, and many larvae and adults of panorpoids. A two-segmented labium appears to be primitive (Walker 1931a). The presence of two segments allows for some labial flexibility in biting-and-chewing forms, but in most holometabolous adults, labial mobility has become reduced and supplanted by various flexible, projecting proboscides. Thus the labial main-body becomes two relatively fixed sclerites associated with formation of a hypostomal bridge, postgenae or a gula (Matsuda 1965) which often anchors a proboscis.

Subdivision of the postlabium into a mentum and submentum, and thus increasing segment number to three (Crampton 1923b, 1925a; Matsuda 1965), occurs in orthopteroids, adult neuropteroids and some holometabolous larvae. A tripartite main-body presumably imparts greater mobility to the "lower lip," resulting in enhanced food-processing efficiency in solid-feeding groups. An opposite trend--reduction of the labium to a single, unspecified sclerite (Crampton 1923a, 1925a)--has occurred in ephemeropteran naiads and in all holometabolous groups (Crampton 1925a, Matsuda 1965). This pattern is consistent with systemic mouthpart reduction in adult, holometabolous larvae that consume solid food. For different reasons, similar labial reduction occurs in nonfeeding strepsipterans and lepidopterans (Bohart 1946b, Scott 1986). A special condition exists for fluid-feeding, beaked homopterans and heteropterans, where the labium con sists only of one segment, the prelabium, which is the basal segment of the beak (Matsuda 1965). The other beak segments may be palpal in origin (Léon 1892, 1897) or more likely, apical endite lobes (Pesson 1944).

5.11.3. Labial Appendages (Character 43)

The typical, unmodified labium bears three pairs of appendages: glossae, paraglossae and palpi. Of these, one, two, or all three pairs may be absent, in various combinations. Frequently an absence is simply an indication of reduction, or it may be associated with a particular labially-involved multielement structure with components from other mouthpart regions. In general, the presence and combination of labial appendages is an indirect indicator of feeding mechanism, insofar that it represents major deviations from a basic labial groundplan. These deviations, such as palpal loss or formation of a silk-producing "ligular" projection, are expressions of particular co-optations, reductions, or even incidental patterns associated with particular feeding strategies.

Three major patterns characterize the presence or absence of labial appendages (see also Matsuda [1965]). First is the generalized state, replete with three pairs of appendages, that occurs in derived apterygotes (archaeognathans and thysanurans), orthopteroids, adult coleopterans and adult hymenopterans. This pattern is associated with various diets exhibiting solid food ingestion. The second pattern is labial absence, occurring in neotenic forms lacking mouthparts and in parasitic dipteran and hymenopteran larvae lacking major mouthpart regions--usually the labium and maxilla--and generally assimilating food cutaneously or by mouthhooks. The third pattern is labial reduction, which has assumed four major themes. These are (i) the glossae only are present, often in the form of a ligula (paraglossae and palpi are absent); (ii) the paraglossae and palpi are present (glossae are absent), (iii) the glossae and palpi are present, the latter often in the form of a labellate structure (paraglossae are absent); and (iv) the labial palpi, or its mofification, the labellum, is present (glossae and paraglossae are absent). These four themes will be described in the following paragraphs.

The presence of only glossae or a ligular process occurs in two groups of insects. It occurs as distal segments in the hemipteroid beak (Heymons 1899, Matsuda 1965; but see Newcomer [1948] for a embryological approach), the wall of the mouthcone in thysanopterans (Matsuda 1965) and sporadically in biting-and-chewing holometabolous larvae (Anderson 1936, Das 1938). In some coleopterous larvae the labium consists of a ligula only and it is associated with wood-boring and carnivorous forms with strong mandibles (Boving 1927b, Boving and Craighead 1931); among dipteran larvae the labium is associated with filter-feeding in aquatic nematocerous larvae (Leathers 1922) and is often termed a "hypostomium" (Lawson 1951). A ligula-only labium also occurs in some brachycerous and cyclorrhaphous larvae, where it is associated largely with carnivorous habits (see Teskey [1976] for examples).

Labia with only paraglossal and palpal appendages occur predominantly among orthopterans, mallophagans, thysanopterans and megalopterans. This pattern is not found in holometabolous larvae and it appears to have no diet-related associations. The presence of a labium with glossae and palpi is associated with adult biting-and-chewing planipennians and coleopterans (Bugnion 1920, Principi 1954). In adult siphonapterans and dipterans this pattern is modified by conjoined labial palpi, which constitute the haustellum in piercing-and-sucking and piercing-and-cutting species (Rothschild 1906, Hoyt 1952). In some dominately surface-feeding cyclorrhaphous and especially brachycerous forms, the labellum forms a major sponging or rasping feeding organ (Peterson 1916). In other adult dipterans, particularly cyclorrhaphans, glossae are absent and the fleshy labellum is the only major labial structure (see Elzinga and Broce [1986] for structural modifications). This pattern also occurs in adult trichopterans, where only palpi are present.

However, in trichopterans the palpi do not form a labellum; instead the prementum is adjoined to a fleshy hypopharynx, the haustorium, to form an analogous sponging organ for feeding (Klemm 1966). In fact, premental-hypopharyngeal fusion occurs to some extent in all holometabolous orders (Matsuda 1965). In lepidopterans, glossae and paraglossae are similarly absent, leaving squamate labial palpi available for odor detection and probably proboscis grooming (Philpott 1925, Scott 1986). Dominantly wood-boring or carnivorous larval species of planipennians, coleopterans, and mecopterans also possess only palpi as labial appendages (Tauber and Tauber 1968, Böving 1927a, Setty 1941, respectively). Adult, mostly necrovorous mecopterans also bear a labium with only palpi as appendages (Hepburn 1969).

5.11.4. Labial Palpus Segmentation (Character 44)

Four fundamental trends characterize labial palpus segmentation in insects. The first trend is the generalized condition of apterygotes and pterygotes, which is a three-segmented labial palpus according to Matsuda (1965), though Kukalová-Peck (1987) has presented paleontological evidence for a primitively eight-segmented structure. However, there has been a second and strong tendency toward reduction in palpus segment number to one or two in larval and adult holometabolous groups. Thirdly, in many obligately fluid-feeding, piercing-and-sucking groups the palpus is lacking. This pattern is repeated in several groups with nonfeeding, ephemeral adults and in certain feeding, usually parasitic, holometabolous larvae. Lastly, in virtually all orders, supernumerary segments characterize some groups (Matsuda 1965)--a feature that is frequently interpreted as secondary acquisition by palpal segment division (Crampton 1928a, Das 1938). Although Das (1938: 38) has claimed that "it is doubtful if the number of palpal segments is of fundamental importance" for larval insects, there nevertheless appear to be some broad associations between palpal presence/absence or segment number and other mouthpart elements for some larval and many adult groups. It is noteworthy that in the few instances where palpal segmentation varies intraspecifically, such as castes in ants (Kusnezov 1954a, 1954b), there is correlation between mandible size and labial palp number, but no correlation between social caste and labial palp size or segmentation (Kusnezov 1954b: 257).

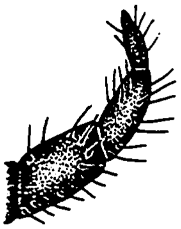
The generalized, trisegmented state is widespread among most insect groups. It is predominant in orthopteroids present in most neuropteroids and many panorpoids and occasionally occurs in holometabolous larvae. The three-segmented palpus occurs in groups that also bear a five-segmented maxillary palpus (four in coleopterans) and is used for solid food manipulation in concert with solid-food ingestion. However, the recurrent trend of labial-segment reduction occurs principally in paleopterans, some hemipteroid groups, some holometabolous larvae and in several groups of fluid-feeding adults. Paleopteran adults and naiads usually bear a one- or two-segmented palpus specialized variously for collecting particulate material or for subduing live prey (Brown 1961, Hakim 1964). In odonatan naiads, a single-segmented palpus becomes a raptorial, jointed claw attached to a labial mask that can be rapidly extruded for striking and retrieving live prey items (Butler 1904, Whedon 1927, Tanaka and Hisada 1980). Palpate hemipteroid groups, especially solid-feeding mallophagans and psocopterans, usually have a one- or two-segmented palpus (see Snodgrass [1905] and Mukerjii and Sen Sarma [1955] for examples). For holometabolous larvae, segment-number reduction occurs as a general feature of mouthpart supression or simplification--i.e. the tendency toward size and segment decrease of nominally long, typically gracile appendages of the adult to short, stubby nubbins minimally used for food manipulation. This is even true for trichopteran, lepidopteran and symphytan hymenopteran forms possessing a prominent labiohypopharyngeal spinneret, wherein the adjacent labial palpus becomes diminutive, aciculate and unsegmented (Das 1938, Jayerickreme 1940).

Complete palpal absence occurs in several major fluid-feeding groups, particularly homopterans, heteropterans and anoplurans, and in stylus-bearing neanurid collembolans (this, of course assumes that the hemipteroid beak is not palpal in origin, as Crampton [1921c] suggests). In these groups the absence of palps is a result of the possession of a tissue-penetrating and fluid-imbibing structure that obviates the need for palps in the manipulation and sensing of solid food. In dipterans and siphonapterans, the relationship is more direct, with the labial palpus actually forming the haustellum. By contrast, piercing-and-sucking forms, such as several coleopteran groups, lack a haustellum; such forms bear labial palps of similar size and segmentation as those of biting-and-chewing forms (see Sen Gupta and Crowson [1973] and Vit [1977] for examples).

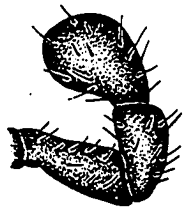
Supernumerary segments occur less frequently than segment reduction, although they are often encountered in thysanopterans, siphonapterans and hymenopterans (Matsuda 1965). In thysanopterans, segment number varies from one to five (Matsuda 1965) whereas in siphonapterans segment number varies from one to 25 (Holland *in* Matsuda 1965). Adult hymenopterans, by contrast, have a four-segmented palpus, when supernumerary segments occur (Crampton 1928a, Winston 1979), which, in apoid forms, is used for forming the tubular funnel through which the glossa squeezes (Snodgrass 1956). Many larval planipennians possess supernumerary segments that have been attributed to "secondary division of the primary three-segmented palpus" (Das 1938: 58).

5.11.5. Labial Palpus Type (Character 45)

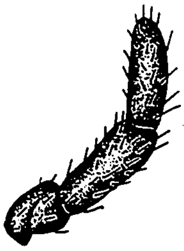
Labial palpi, like maxillary palpi, are major mouthpart appendages involved almost always in the sensing, probing, and manipulation of food in the external environment (Gangwere 1960, 1965; Chauvin and Faucheux 1981; Chapman 1982; see Staedler 1977 for a review). The generalizations established for maxillary palpi (see Section 4.10.5) can be transferred directly to the labial palpi of many groups and particularly for those bearing filiform, clavate, and serrate types (Fig. 24). In other groups labial palpi have become modified significantly, such as the claws on the labial mask of odonatan naiads (Munscheid 1933), or as a major component in a multielement food acquisition organ for the piercing, sponging, rasping, or squeezing of tissue-embedded or surface fluid into the cibarium of holometabolous adults (Graham-Smith 1911, 1930; Harder 1982; Smith 1985). Because of these and other major patterns of palpal modification, five major trends characterize labial palpal development of insects from the generalized palpus condition: (i) palpi modified for aquatic filter-feeding in ephemeropteran naiads, (ii) clawlike palpi of the labial mask of odonatan naiads and the "trophic basket" of odonatan adults, (iii) the reduced palpi of holometabolous larvae, (iv) a varied assemblage of specialized palpal types



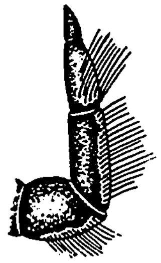
B. MUCRONATE.
EPH: *Ephemerella* sp.
Naiad, [Murphy 1922].



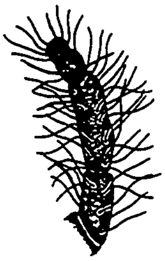
C. CLAVATE.
TYN: *Thermobia domestica*
(Packard). Adult, [Walker, 1931].



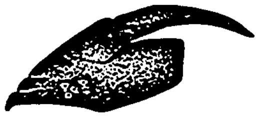
D. FILIFORM.
PHA: *Necrosia sparaxes*
Westwood. Adult, [Gangrade 1965].



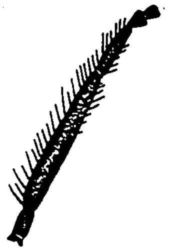
E. PECTINATE.
EPH: *Lepeorus goyi*
Peters. Naiad, [Schonmann 1981].



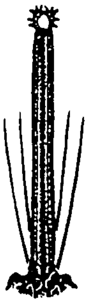
F. PENICILLATE.
COL: *Scarabaeus sacer*
Linneaus. Adult, [Bertin 1923].



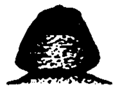
G. CHELATE, SINGLE HOOK.
ODO: *Aeshna cyanea*
Muller. Naiad, [Munscheid 1933].



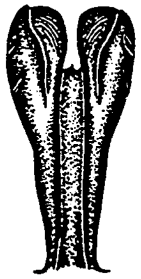
H. PROLONGED-DIMUNITIVE.
HYM: *Apis mellifera*
Linneaus. Adult,
[Snodgrass 1942].



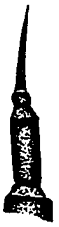
I. TUBULATE.
DIP: *Strebla vespertilionis*
Fabricius. Adult, [Jobling 1929].



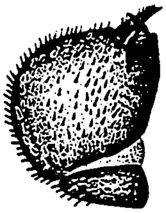
J. PAPILLATE.
HYM: *Bracon tachardiae*
Cameron. Larva, [Glover 1934].



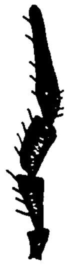
K. LABELLATE.
DIP: *Tabanus* sp. Adult,
[Peterson 1916].



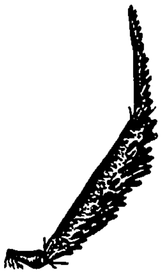
L. ACICULATE.
LEP: *Ectoedemia heinricki* Busck. Larva,
[DeGryse 1915].



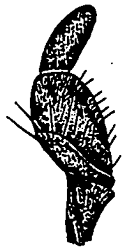
M. CHELATE, TWO HOOKS.
ODO: *Aeshna cyanea*
Muller. Adult, [Munscheid 1933].



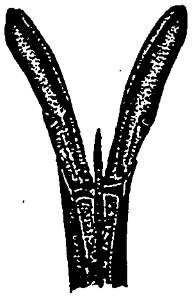
N. SERRATE.
TRI: *Polycentropus* sp.
Adult, [Deoras 1943].



O. SQUAMATE.
LEP: *Oecophora bractella*
(Linneaus). Adult, [Clarke 1941].



P. ENLARGED MIDDLE SEGMENT.
MEC: *Panorpa communis*
Linneaus. Adult, [Heddergott 1938].



Q. APPRESSED.
DIP: *Exoprosopa*, sp.
Adult, [Peterson 1916].

FIGURE 24. Character-states of Character 45: labial palpus type. Not drawn to scale.

in fluid-feeding holometabolous adults and (v) palpal absence in various piercing-and-sucking, nonfeeding and parasitic groups.

The generalized condition for labial palpi is associated with various orthopteroid, adult neuropteroid, many adult panorpoid and hymenopteran insects. The pterygote generalized condition comprises the filiform palpus type and its immediate derivatives, the clavate and serrate types. These three palpal types represent changes in segment shape rather than an overhauling of entire palpus shape or vestiture to perform a new function. Blackwelder (1936) has described representative labial palpi from a diverse family of coleopterans, the Staphylinidae, illustrating a few structural deviations from the typical generalized condition. The sensory functions of generalized palpi have been documented primarily for orthopterans, especially grasshoppers (Thomas 1966, Chapman and Thomas 1978) and crickets (Klein and Müller 1978). Although these sensory functions occur in the structurally divergent palpal types borne especially by adult holometabolous groups (Jayewickreme 1940, Wilczek 1967), such palpi have become elements in other, major mouthpart apparati for food acquisition, including combing, grasping, sponging and siphoning.

Many aquatic microvorous and detritivorous larvae, especially ephemeropteran naiads, bear flattened setose to spinose palpi specialized for filter-feeding or brush-sweeping (for synoptic studies see Usinger 1956, McCafferty and Provoshna 1981 and Merritt and Cummins 1984). Several recent studies have documented the role of palpal and other mouthpart setae as filtering fans, collecting seives, or grazing brushes in the interception and collection of suspended and epibenthic detritus (Braimah 1987a, 1987b).

By contrast, odonatan naiads possess a single-segmented, flattened, falcate palpus articulating on the distal ligular margin, serving as a retractile claw for grasping live prey at the end of a rapidly protrusible labial mask (Snodgrass 1954). In adult odonatans a similar palpal type occurs, characterized by a movable hook or modified palpus that articulates against an immovable process (Hakim 1964). This grasping structure functionally mirrors the chelicerae found in mites (Metcalf et al. 1962) and is used to secure prey items. Analogous structures occur as prosthecate mandibles of a few beetle genera (Boving and Craighead 1931: 253; Dajoz 1976).

Continuing the widespread pattern of mouthpart reduction in larval holometabolous insects is palpal type, which assumes three major diminutive structures: (i) a papillate or stubby form, (ii) an aciculate form resembling a seta or spine and (iii) a mucronate form consisting of two or three narrow segments that taper distally. Papillate palpi are found in some apterygotes (Bitsch 1952), some hemipteroids (Smithers 1972), but predominantly in coleopteran and panorpoid larvae (for examples, see Anderson 1936 and Peterson 1948, 1951). Mucronate palpi are encountered in coleopteran and some panorpoid larvae (Gage 1970), whereas aciculate palpi are confined to adult dipterans and larval lepidopterans. A common feature among all three palpal types is their strong association with the labiohypopharyngeal spinneret in trichopterans, lepidopterans and symphytan hymenopterans (Jayewickreme 1940, Lorenz and Kraus 1957, Badcock 1961). For coleopteran, mecopteran and siphonapteran larvae, papillate and aciculate palpi are associated with solid-food ingestion and generally carnivorous or necrovorous diets.

Adult holometabolous groups exhibit a diverse assemblage of palpus types that fall into four major patterns: (i) various modifications in shape and denticulation of a haustellate palpus in dipterans and siphonapterans, (ii) lepidopteran palpi densely covered with hairy or scaly vestiture (Lee 1987), (iii) an excavate, elongate palpus of apoid hymenopterans and (iv) palpi with an enlarged middle segment housing special sensory organs. Nematoceran dipteran palpi are two-segmented, stylet-encompassing structures employed for directing long stylets into tissues of various kinds (Gordon and Lumsden 1939). The haustellate palpus has been structurally modified into a fleshy, microtraceate labellum that has abandoned the function of directing stylets and has acquired the function of sponging fluids or particles (Schuhmacher and Hoffmann 1982) without tissue laceration (after Snodgrass 1943). The labellum, in turn, has been secondarily modified into a tissue-rasping structure by modification of distal labellar denticles into short, acuminate, often spinose structures (Senior-White 1922-23, Makhan'ko 1973, Zaitzev 1982) that abrade dermal tissue for uptake of oozing subdermal fluids (Broadhead 1984). Notably, among congeneric species, labellae have been modified into either sponging or rasping organs, depending on prestomal tooth development (Broce and Elzinga 1984, Elzinga and Broce 1986). An alternative route of labellar modification is prolongation of the labellum into a tubular proboscis surmounted by a battery of terminal spines for piercing tissue (Gordon et al. 1956).

This acquisition effectively changed the fleshy labellum into a semi-rigid "stylet" for deep penetration into tissue, especially in sanguinivorous and parasitic dipterans (Jobling 1926, 1928a, 1929).

Palpi of adult lepidopterans generally have a densely suffused vestiture of hairs or their structural derivative, scales. Various sensillae are located on these palpi and they are probably used for sensing odors associated with nectar (Portier 1949, Scott 1986). Rare palpal modifications have been documented by Philpott (1925) wherein the terminal segment is modified into a strygil, presumably for grooming the proboscis or antennae. Although apoid hymenopterans have palpi that appear similar in shape to lepidopteran palpi, their principal function is to form a tube with the galeae for the extraction of fluid food by a sucking pump (Snodgrass 1956).

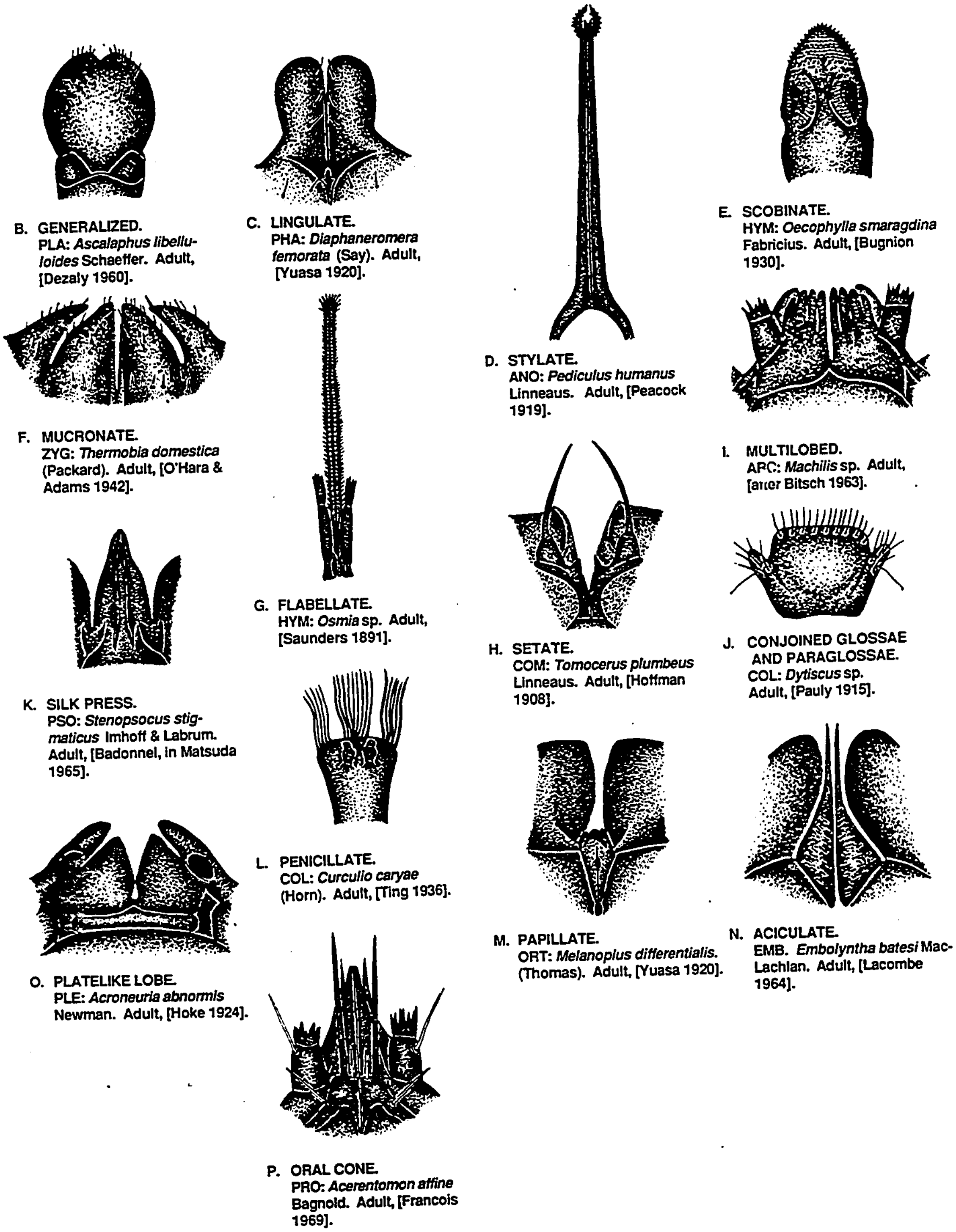
The last trend of labial palpus modification is its complete absence or vestigiality in several groups. These groups include mandibulate collembolans, where it probably is secondarily lost (Adams and Salamon 1972), the piercing-and-sucking hemipteroid anoplurans, homopterans and heteropterans, characterized by secondary palpal loss (Hamilton 1981), and various strepsipterans and holometabolous larvae which have undergone mouthpart reduction usually as a consequence of a parasitic life-style (Kinzelbach 1966; for examples see Gouin 1959 and Grandi 1959).

5.11.6. Glossa Modifications
(Character 46)

The glossa is a mesially-located, distal, labial lobe involved, in part, as a lower "lip" in biting-and-chewing insects. In its generalized form the glossa bears many sensory structures involved in tactile sensation, gustation, and manipulation of food. These functions have been documented for orthopterans (Gangwere 1960, 1966; Chapman and Thomas 1978), isopterans (Richard 1951), and larval and adult coleopterans (Corbière 1967, Forsythe 1983). Glossae are not as widespread throughout the orders of insects as are their maxillary homologues, the laciniae. Glossae are present mostly in solid food-feeding hemipteroids, adult planipennians and adult coleopterans, frequently as a conjoined structure, the ligula (*vide infra*; Matsuda 1965). Notably, glossae are absent in many (probably most) holometabolous adults, including megalopterans, raphidiopterans, strepsipterans, mecopterans, trichopterans, lepidopterans, and siphonapterans. Although glossae are sporadically absent in the larvae of planipennians, coleopterans and hymenopterans, in many larval panorpoid forms the prementum and glossae are inextricably fused to the hypopharynx to form a composite organ involved in spinning silk, rasping hard substrates, or other functions. In a few forms, such as orthopterans, glossae are vestigial and are supplanted by paraglossae as the major labial organs of food manipulation (Thomas 1966).

When considered in its total range of structural variation (Fig. 25), four major patterns characterize glossal form: (i) generalized glossal or ligulate lobes or their immediate derivatives, (ii) various

GLOSSAE MODIFICATIONS



B. GENERALIZED.
PLA: *Ascalaphus libelluloides* Schaeffer. Adult, [Dezaly 1960].

C. LINGULATE.
PHA: *Diaphaneromera femorata* (Say). Adult, [Yuasa 1920].

D. STYLATE.
ANO: *Pediculus humanus* Linneaus. Adult, [Peacock 1919].

E. SCOBINATE.
HYM: *Oecophylla smaragdina* Fabricius. Adult, [Bugnion 1930].

F. MUCRONATE.
ZYG: *Thermobia domestica* (Packard). Adult, [O'Hara & Adams 1942].

G. FLABELLATE.
HYM: *Osmia* sp. Adult, [Saunders 1891].

H. SETATE.
COM: *Tomocerus plumbeus* Linneaus. Adult, [Hoffman 1908].

I. MULTILOBED.
ARC: *Machilis* sp. Adult, [after Bitsch 1963].

J. CONJOINED GLOSSAE AND PARAGLOSSAE.
COL: *Dytiscus* sp. Adult, [Pauly 1915].

K. SILK PRESS.
PSO: *Stenopsocus stigmaticus* Imhoff & Labrum. Adult, [Badonnel, in Matsuda 1965].

L. PENICILLATE.
COL: *Curculio caryae* (Horn). Adult, [Ting 1936].

M. PAPILLATE.
ORT: *Melanoplus differentialis*. (Thomas). Adult, [Yuasa 1920].

N. ACICULATE.
EMB. *Embolyntha batesi* MacLachlan. Adult, [Lacombe 1964].

O. PLATELIKE LOBE.
PLE: *Acroneuria abnormis* Newman. Adult, [Hoke 1924].

P. ORAL CONE.
PRO: *Acerentomon affine* Bagnold. Adult, [Francois 1969].

FIGURE 25. Character-states of Character 46: glossal modifications. Not drawn to scale.

modifications for more specialized modes of solid food-feeding, (iii) various modifications for fluid-feeding on deep tissue or surface liquids and (iv) reduction of the glossae to diminutive processes, culminating in glossal absence. (I am using the term "ligula" to refer to an undivided, conjoined glossal lobe or to any other region of the labium distad of the labial palpus; it may include parts of the prementum.)

The generalized condition consists of a simple, fleshy, divided or ligulate lobe with sensory organelles and a modicum of setation. This form exists in apterygotes, some orthopteroids, psocopterans, larval megalopterans, the adults and larvae of coleopterans, nematocerous and brachycerous dipterans, and hymenopterans. Immediate derivatives of this basic form are (i) subdivision of each glossa into two similar, generalized lobes in archaeognathans, (ii) the formation in phasmatodeans and coleopterans of a spatulate lobe from each glossa, characterized by a narrowing of the basal attachment region and (iii) fusion of each glossa to the paraglossa in odonatans, mallophagans and adult coleopterans. These four character-states are associated with solid-food feeding.

More distinctive glossae are associated with solid-food feeders that are specialized on particular diets. A scrobinate glossa or ligula is found among omnivorous blattoids (Bugnion 1920) and various symphytan hymenopterans, especially formicids (Bugnion 1930). For hymenopterans, its function as "a rasping and licking organ" has been mentioned for chalcids by Bucher (1940: 236), and Seghal (1963: 165) described the anterior glossal surface of a vespid as "bearing rows of very small setae having [a] rasping function." A common structural type is a densely setate lobe that is characterized by a profusion of hair across a broad ligulate glossal surface, as opposed to the penicillate condition--a specific collection of elongate, specialized setae modified into a compact brush or broom for licking or sweeping particulate matter. Setate glossae and ligulae are widespread in adult and immature terrestrial coleopterans with eclectic diets, or among filter-feeding aquatic ephemeropteran naiads (Schonmann 1981). By contrast, penicillate glossae have a more restrictive, terrestrially based, function of capturing particulate material, especially pollen (Schicha 1967, Barth 1985) and spores (Lawrence and Newton 1980) among anthophilous and mycophilous coleopterans. For beetles, penicillate glossae or cleft ligulae (Goldman 1933) bear specialized setae for entrapping and moving pollen or spores toward the cibarium, such as the sticky *Trompenborsten* and spoon-shaped *Loffelborsten* described by Schicha (1967). These structures are coordinated with similarly penicillate or otherwise setate galeae and mandibles for the transportation of particulate food to the mouth (Schicha 1967, Fuchs 1974). The occurrence of glossal-paraglossal fusion, resulting in a broad, lower plate, is found in odonatan adults and naiads in conjunction with raptorial labial palpi used for predation (see Popham and Bevans 1979). A glossal-paraglossal plate also occurs sporadically in adult coleopterans and may be associated with fungivory.

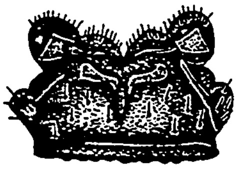
The labiohypopharyngeal spinneret of trichopterans, lepidopterans and symphytan hymenopteran larvae is a silk-secreting apparatus formed ventrally by a distal, axial lobe of the labium that is dorsally adnate to the hypopharynx (Snodgrass 1935). This structure is used by aquatic hydropsychoid caddisflies to spin particle-trap nets for filter-feeding (Wallace and Malas 1976; Wallace and Merritt 1980) and pupal cocoons in obligately herbivorous caterpillars and sawflies (Richards and Davies 1977). Unlike the strong association between diet and the spinneret, mucronate glossae are found in various insect groups lacking a dietary theme. Two basic structures occur in glossae or ligulae specialized for fluid-feeding. First are structures associated with piercing-and-sucking, which are (i) the "ventral sting" or stylet in sanguinivorous anoplurans (Hirsch 1987), (ii) various wall sclerites forming the mouthcone of thysanopterans (Heming 1978) and the oral cone of proturans (Francois 1969) and (iii) the stylet-guides of coleopterans (Besuchet 1972, Dajoz 1976). Secondly, conjoined glossae form a prolonged organ for mopping nectar in apoid hymenopterans (Snodgrass 1956). This prominent organ bears numerous ramose hairs (Bryant 1884) to which droplets of nectar cling, the distalmost of which are modified into a spoon-shaped structure for cupping nectar from flower sources (Liu 1925, Barth 1985). (This glossa is mirrored by similarly hair-laden, very long labellae of nectarivorous tabanid dipterans [Mitter 1918].)

Glossae that are reduced or absent occur in three basic forms. They may be insignificant, diminutive, papillate lobes, often over-shadowed by well-developed, lobate paraglossaae, found in orthopterans and embiopterans (see Yuasa [1920] and Rahle [1970] for examples). Alternatively, glossae may bear a few spinose, sclerified projections, a feature found in predatory coleopteran adults (Pauly 1915, Weinreich 1968, Forsythe 1983). Finally, glossae may be lacking altogether--a widespread pattern found in dermapterans, advanced hemipteroids and particularly in holometabolous groups. Notably, glossal absence characterizes entire groups, such as larval planipennians and adult trichopterans, lepidopterans and cyclorrhaphous dipterans.

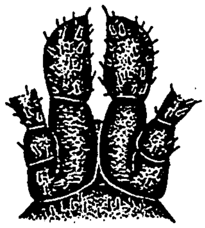
5.11.7. Paraglossae Modifications (Character 47)

Paraglossae are lobate appendages occurring laterad of the glossae. Although they are encountered less frequently than glossae among insect groups, they nevertheless often replace glossae as the major labial organ for manipulating food. Paraglossae are frequently very similar in overall shape and vestiture to glossae--a feature that is not paralleled by the analogous maxillary lobes, the galeae and laciniae. Because of these features, the repertoire of paraglossal modification is significantly less than that of the glossae. (Interestingly, three of the 11 paraglossal character-states are restricted to hymenopterans because of appendage structural variation in the protractile and retractile labiomaxillary apparatus.) Although the scope of paraglossal modification is relatively limited for a mouthpart appendage (Fig. 26), four major patterns can be discerned. They are (i) a generalized or structurally equivalent type, (ii) types equipped for processing more specialized solid-food diets, (iii) types used for obtaining fluid foods and (iv) paraglossal absence or near-vestigiality.

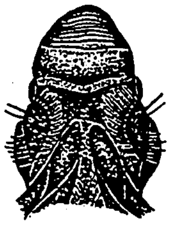
The generalized paraglossa comprises an unmodified, fleshy lobe used in sensory reception and manipulation of solid food (Gangwere 1966, Thomas 1966, Chapman 1982). For biting-and-chewing orthopteroids, the paraglossae are the principal lobes of the lower lip and consist of a



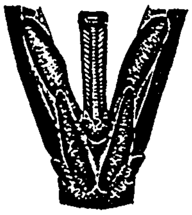
B. **GENERALIZED.**
PSO: *Psocus confraternus* Banks. Adult, [Cope 1940].



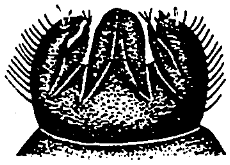
C. **LINGULATE.**
DER: *Labidura riparia* (Pallas). Adult, [Kadam 1961].



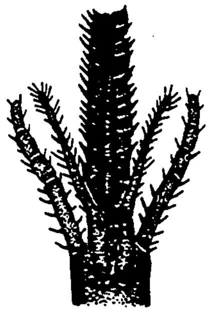
D. **PECTINATE.**
HYM: *Messor structor* Latreille. Adult, [Bugnion 1930].



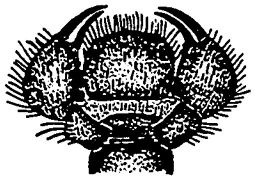
E. **PALPIFORM.**
HYM: *Bombus* sp. Adult, [Saunders 1891].



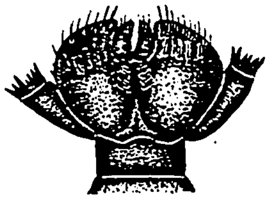
F. **MUCRONATE.**
TRI: *Philanisus plebius* (Walker). Larva, [Leader 1976].



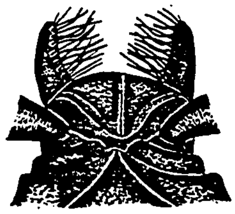
G. **FLABELLATE.**
HYM: *Nomia melanderi* Cockerell. Adult, [Stephen, Bohart & Torchio 1969].



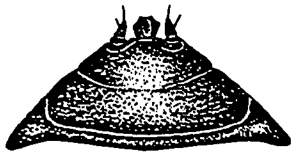
H. **CONJOINED GLOSSAE & PARAGLOSSAE.**
ODO: *Onychogomphus ardens* Needham. Adult, [Chao 1953].



I. **PLATELIKE LOBE.**
EPH: *Potamanthus luteus* (Linneaus). Naiad, [Landa 1969].



J. **PENICILLATE.**
COL: *Megalodacne fasciata* Fabricius. Adult, [Williams 1938].



K. **ORAL CONE.**
THY: *Cephalothrips yuccae* Hinds. Adult, [Peterson 1915].

FIGURE 26. Character-states of Character 47: paraglossal modifications. Not drawn to scale.

robust, unmodified lobe usually in carnivorous groups, and a more gracile, spatulate structure in herbivorous to omnivorous groups (Yuasa 1920, Walker 1931a). For some adult coleopterans, the paraglossae, when present, is a spatulate structure (Williams 1938, Crowson 1981). Mucronate, or tapering palpi are found in thysanurans and mantodeans (Levereault 1936, O'Hara and Adams 1942).

Modifications of paraglossae for processing solid foods include the pectinate, penicillate, generalized-ligulate and palpiform types. Pectinate paraglossae occur in adult aculeate hymenopterans, especially ants, and are presumably used for transferring particulate or solid food material anteriorly (for examples, see Bugnion 1930). These paraglossae are rigid, coarsely setate to spinose and bear setation similar to that of the pectinate mouthparts of aquatic forms (Bugnion 1930). A finer density of vestiture and a smaller setal size typifies penicillate paraglossae, which dominately occurs in ephemeropteran and plecopteran naiads (Claassen 1931, Landa 1969) that are brush-feeders on stream detritus. Notably, this is a reversal of the typical pattern, wherein penicillate mouthparts are associated with terrestrial particle feeders and pectinate mouthparts with aquatic filter-feeders. Another paraglossal modification is fusion of the paraglossae to the glossae to form a broad ligulate expansion. In predatory odonatan adults and naiads, such a plate-like structure is used as a surface against which the raptorial claws abduct in the securing of prey (Tanaka and Hisada 1980). For adult coleopterans, this ligulate structure occurs in groups of diverse dietary habits (Williams 1938; Crowson 1981). Finally, paraglossae are rarely modified into palpiform structures, such as the labial strike mechanism of the adult staphylinid coleopteran *Stenus*; it is involved in subduing live prey as the prey is impaled by glossal spines (Schmitz 1943, Weinreich 1968).

Paraglossae are modified for liquid-feeding in three major ways: (i) participation in formation of an oral tube for directing stylets, (ii) as a basal glossal coverlet for chanelling salivary fluids and (iii) formation of an elongated, flabellate tongue. The first and last of these modifications parallel patterns found in glossae (see Section 4.11.6). Incorporation of paraglossal sclerites into the mouthcone wall of thysanopterans has been mentioned by Heming (1978). Among adult aculeate hymenopterans, the paraglossae are membranous, linear structures semicircular in cross-section, serving as coverlets for the basal part of the glossal tongue for guiding salivary secretions into the ventral glossal channel (Snodgrass 1935). Paraglossae are often hairy (Michener 1944) and can be as long as the glossa in some bees (Winston 1979), presumeably assisting the glossa as a flabellate, nectar-mopping organ (for examples, see Demoll 1908).

The fourth pattern is widespread paraglossal absence among collembolans, advanced hemipteroids and many holometabolous larvae. Paraglossae are absent in raphidiopterans, megalopterans, planipennians, most superfamilies of coleopterans (including hydrophiloids, scarabaeoids, elateroids, cantharoids, cucujoids and curculionoids), strepsipterans, mecopterans, siphonapterans, dipterans, trichopterans, lepidopterans and larval symphytans. Paraglossae, and to a lesser extent glossae, are structures that are suppressed to some degree in almost all insect groups exclusive of apterygotes, paleopterans and orthopteroids.

5.11.8. Labial Palpus
Aspect Ratio (Character 48)

Labial palpus aspect ratio is assessed as the ratio of average segment width to total palpus length, excluding the palpifer. Based on the magnitude range of these ratios, labial palpus length was divided into very long, long, intermediate, short, and absent character-states, with a special category reserved for forms with labellate or labellate type palpi. In general terms, there are only four major patterns of labial palpus length. They are (i) the most widespread trend of mostly generalized labial palpi (see Section 4.11.5), comprising a gradational series ranging from intermediate to long in length, (ii) rare occurrences of very long palps, (iii) a commonly occurring trend of short palps and (iv) sporadic occurrences of apalpate forms in a few specialized groups. These trends, in turn, bear subpatterns that characterize taxonomically discrete groups.

The taxonomically widespread and numerically abundant assemblage of labial palpi that gradationally ranges from long to intermediate is found in principally orthopteroid, neuropteroid and adult panorpoid insects. This assemblage is so dietarily diverse that no association exists between palpal length and diet. Two subpatterns, however, are evident: (i) advanced apterygotes--archaeognathans and thysanurans--uniformly bear intermediate-length palpi and (ii) orthopterans and closely-related orders bear long palpi. By contrast, the distribution of very long palpi does exhibit a pattern. It occurs in fluid-feeding siphonapterans, dipterans, lepidopterans and aculeate hymenopterans. This distribution is congruent with, but more taxonomically restrictive than, the occurrence of very long maxillary palps, the latter which also characterizing certain orthopterans, larval coleopterans and adult mecopterans (see Section 4.10.6). Undoubtedly, in siphonapterans and dipterans, labial palpus length is associated with its intimate association with a very long labium used for housing stylets (Crampton 1925a, Snodgrass 1959), which among siphonapterans can range up to a 25 segmented structure (Snodgrass 1946, Holland *in* Matsuda 1965). Among lepidopterans and aculeate hymenopterans, very long palpi are associated with prolonged proboscides and the attendant functions of grooming (Scott 1986) or formation of a food tube (Harder 1982).

The distribution of short labial palpi occurs predominantly in a few major groups, each which has a rather uniform dietary theme. Short palpi occur in primitive apterygotes, especially predominantly necrovorous proturans and diplurans. They also occur in palpate, mostly solid-food-feeding hemipterans, particularlly psocopterans, mallophagans and thysanopterans. Among aquatic naiads of ephemeropterans, plecopterans and trichopterans, short palpi are usually flattened, broad and with distinctive vestiture for collecting suspended particulate material or grazing on epibenthic algae or detritus (for examples, see Landa 1969).

Adult cyclorrhaphous dipterans, which feed on surface and shallow subdermal fluids, also possess short, albeit structurally divergent, labial palps that coalesce to form a fleshy labellum (Dethier 1959). The most common occurrence of short palpi is among larvae of every major holometabolous order, where they constitute part of the pervasive syndrome of mouthpart reduction (Snodgrass 1935), and in many of these groups they appear as nubbins with a few sensory setae (for examples, see Jayewickreme 1940, Peterson 1951, Lorenz and Kraus 1957).

Complete labial palpal absence occurs as a major feature in two insect groups. First, it is part of the *Baupläne* of fluid-feeding hemipteroid insects (anoplurans, homopterans and heteropterans) characterized by incorporation or wholesale transferral of the labium into a stylet-encompassing, segmented-beak (Hamilton 1981). Secondly, palpal absence is associated with extension of the trend of mouthpart reduction in holometabolous larvae and strepsipterans (*vide supra*) and oftentimes is a consequence of labial supression (Kinzelbach 1966; Teskey 1981e).

5.11.9. Labial Participation in a Multielement Mouthpart Structure (Character 49)

Although the labium exhibits many structural parallels to the maxilla--e.g. palps and mesial axial lobes--it nevertheless enters into more multielement complexes than the maxillae. The structural diversity of the mouthpart apparati in which the labium is a major participant is 1.5 times that of the maxilla (compare Characters 40 and 49). In many groups, the labium has been an integral structure in the development in mouthpart innovation, particularly the haustellum for heteropterans and dipterans, the protrusible mask of odonatan naiads and the glossa-wringing maxillolabial complex in hymenopterans. When this diversity is surveyed, six large-scale patterns appear to characterize multielement labial development. These are (i) the generalized state without cooptation, (ii) formation of a haustellum of various kinds and their immediate derivatives, (iii) formation of a labellum or similar structure and their immediate derivatives, (iv) various other structures associated with adult feeding on surface fluids, (v) modifications of the basic mandibulate condition of adults and (vi) co-optation with the hypopharynx to form a spinneret in some holometabolous larvae.

The most common pattern of labial structure is the generalized condition, consisting of a segmented palp and usually one or two pairs of median lobes. This type is found in some apterygotes, orthopteroids, biting-and-chewing hemipteroids, neuropteroids, many holometabolous larvae and some adult hymenopterans. Virtually all taxa exhibiting generalized labia are solid-food ingesters, albeit of diverse dietary habits. There are gradational morphological series between the generalized condition and some multielement types, principally the labral cone of some adult coleopterans (Crowson and Sen Sarma 1973, Besuchet 1972) and rostrum formation in adult planipennians (Crampton 1921c).

Labial participation in a haustellum prominently occurs in several unrelated hemipteroid and panorpoid groups. This co-optation occurs either by incorporation of the labium as part of the wall sclerites in various conical haustella, or formation of an entirely labial structure, palpal or nonpalpal in origin, to house piercing stylets. The mouthcone of herbivorous or pollinivorous thysanopterans is a compact, composite structure integrating sclerites from the labrum, maxilla, labium and head capsule in the construction of a short, distally tapering, apertuate cone. By contrast, haustellum-bearing hemipteroids bear a one- to four-segmented, entirely labial haustellum, known as the beak, used for fluid-feeding on biologically bound tissue. Siphonapterans also bear a similar structure, although it consists of conjoined palpi and segment number can be as high as 25 (Matsuda 1965). Also labial in origin, the haustellum of nematocerous and brachycerous dipterans is, by contrast, unsegmented, fasiculate and does not entirely encompass the stylets, although it does entrain stylets during tissue penetration (Gordon and Lumsden 1939). The various enrolled labial extensions that form stylet guides are not true sheathing haustella and occur among various adult coleopterans. Notably, the labial palpus and associated structures assist the galeal "stylet" of adult noctuid lepidopterans in piercing the skins of fruits and even bovid ungulates for fluid feeding (Srivastava and Bogawat 1969; Bänziger 1980). A similar structure occurs in several sanguinivorous, cyclorrhaphous dipterans (Jobling 1926, Schaefer 1979).

A fleshy, hypognathous structure used for adsorbing surface fluids is found in the adults of four major insect groups. In three of these groups this structure is composed of the labium or is indirectly supported by labial elements. In dipterans and some mecopterans, modified, distally-expanded palpi, often termed a labellum, are used for sponging exposed fluids (McAlpine 1981) and particles (Schuhmacher and Hoffmann 1982). In adult trichopterans, a prominent fleshy hypopharynx is used as a labellum-like organ for sponging surface fluids (Crichton 1957). Although gryllid orthopterans bear a similar, expansive hypopharyngeal organ (Rietschel 1953), it is deployed independent of the labium. A major modification of the dipteran labellum is its modification into a denticulate, rasping organ, wherein microtracheal denticles have been converted into small, piercing spines for abrading dermal tissue (Broadhead 1984).

Labial elements are involved with various other adult feeding organs of surface fluids, particularly the glossa of apoid hymenopterans and the siphon of lepidopterans. The maxillolabial complex of hymenopterans involves a variously prolonged glossa which, when retracted, passes through a constricting "tube" formed by maxillary galeae and labial palpi for the wringing of nectar into the cibarium (Snodgrass 1942). The paraglossae act as a cover-plate for the directing of salivary secretions into the glossal furrow (Snodgrass 1935). By contrast, the labium is only a supportive element for the anchoring of the maxillary siphon in lepidopterans (Schmitt 1938).

Multielement complexes modified from adult biting-and-chewing mouthparts include the structurally disparate rostra of curculionoid coleopterans, mecopterans and some nemopterid planipennians; the maxillolabial apparatus of some hymenopterans; and the labial mask of odonatan naiads. The prognathous elongation of the anterior head capsule is a notable feature in some coleopterans (Crowson 1981); it is conspicuous among curculionoids (Ting 1936) where it is used in probing for hard foods, especially seed, grain and pollen. The labium contributes to the ventral wall of this structure and bears, with maxillary elements, terminal movable mouthparts (Dennell 1942). By contrast, mecopterans and nemopterid planipennians differ by having movable mouthpart elements that originate basally and a rostrum consisting of prolonged mouthpart elements (Otanes 1922). Mecopteran and some planipennian rostra also bear a strong clypeal pump (Heddergott 1938) and are associated usually with a fluid, necrovorous diet (Hobby and Killington 1934). The maxillolabial complex of adult hymenopterans lacking long, glossal tongues (e.g. ants) processes eclectic diets (Wheelr 1910). The protrusible labial mask of predaceous odonatan naiads is a nearly unique structure, matched only by a similar structure in the similarly predaceous adult staphylinid coleopteran *Stenus*. The mask consists of elongate postmental and premental sclerites that are connected by robust musculature and are used as a sling for the rapid capture of nearby prey items (Snodgrass 1954). Capture is effected by terminal palpal claws that abduct against the ligular surface for securing prey (Popham and Bevans 1979).

Larvae of trichopterans, lepidopterans and symphytan hymenopterans bear a labiophyopharyngeal structure, the spinneret. The spinneret produces silk threads that are used variously as a net for capturing suspended detrital particles in water (Wallace and Malas 1976) or for constructing pupal cocoons by many herbivorous, terrestrial larvae.

The labium forms an essential multielement component in many mouthpart complexes. In its unco-opted state, it mechanically and sensorially serves as a "lower lip" in biting and grazing insects. In derived groups the labium has diverse associations, principally with the adjacent maxillae and hypopharynx for feeding on surface fluids. In most piercing forms, the labium comprises the entire haustellum, housing various combinations of mandibular, maxillary, hypopharyngeal and epipharyngeal stylets. In nonhaustellate groups such as proturans, thysanopterans and some coleopterans, the labium, labrum and other sclerites form a robust mouthcone or other stylet guide for directing stylet movement.

5.12. Summary Statements

In Chapter 4 I have attempted to demonstrate how various characters and character-states relate to food acquisition, food processing and diet. Although at a gross, qualitative level it is facile to speak of structure and function as reciprocal features of each other--for example a butterfly's siphoning proboscis, a fly's sponging labellum, or a beetle's biting mandibles--such equations are less evident at the level of the character or character-state (see Appendix A). For example, how are maxillary palpi associated with diet or feeding? Could it be that maxillary palpi are structured independent of diet? (And if so, such a character should be minimally informative in the data-set.) Alternatively, as the documentation of this section has shown, considerable ecologic, behavioral and taxonomic data exist concerning the relationship between gross mouthpart and head structure, and feeding and diet. For example, adult cyclorrhaphous flies are almost always associated with surface fluid-feeding whereas hemipterans obligately pierce tissue by the aid of stylets; orthopteroids are biters-and-chewers that consume solid food. The list is quite extensive. As Smith put it:

> Virtually anything potentially nutritious provides food for one insect or another . . . But things nutritious come in many forms: both physical (liquids, free or contained; solids, in bulk, particulate, soft, hard, homogenous, heterogenous) and animate (active prey, hosts with defence systems). Thus we may expect to find in the adaptive radiation of insects a diversity of feeding mechanisms to match the diversity of food sources. Fortunately evolution is constrained both by physical law and by its raw genetic material. Insect mouthparts are all adaptations of the same set of basic appendages. One consequence is that just as we can classify the numerous insect species into far fewer groups, each sharing common characteristics, so we can reduce feeding mechanisms into manageable sets (Smith 1985: 34).

A fundamental assumption in this section is that these "manageable sets" are reducible to a large suite of structurally definable, discrete characters and character-states. Considerable data, marshalled in this section, support this view: labial palps are either absent or are co-opted into the haustella of stylate forms; forms with tubular or chanelled mandibles are obligately insectivorous and predaceous. This reduction of major mouthpart/head ensembles into smaller structural units operationalizes (i.e. makes explicit) and thus permits categorization of described insect mouthparts beyond the anecdotal or general qualitative assessment (see also functional analyses in Section 2.2).

Perhaps a more robust approach is a numerical quantification of morphologically relevant mouthpart measurements, followed by a multivariate analysis of mouthpart form. Although in principle this is desirable, there are several practical drawbacks to such a study. First, such a study would minimally require a tenfold increase in time needed for measuring mouthpart and head dimensions, when compared to the present study. Second, there is the widespread unavailability of such data, resulting in a pronounced decrease of taxonomic representation in the data-set. Third, such a study would increase the number of variables in the data-matrix variables at least fivefold, perhaps significantly risking the unavailability of relevant computer programs for data processing. Lastly, such an increase in quantitative precision may not result in a commensurate increase in analytic resolving power.

A coarse-grained synopsis of the data-set character-states indicates that major and minor patterns are present based on (i) the numbers of genera or species possessing particular associated character-states and (ii) structural divergence of the character-states themselves. First are the major patterns. A vast, ordinally diverse assemblage of apterygotes, orthopteroids and neuropteroids bear generalized mouthparts with chewing mandibles. Second, typical biting-and-chewing mouthparts of holometabolous larvae are often reduced for very different functions--such as the mouthhook apparatus of some cyclorrhaphous flies and the labiohypopharyngeal spinneret of some panorpoids. Third, adult fluid-feeding hemipteroids and holometabolans have acquired a diverse array of mouthpart body-plans that are often highly correlated with taxonomy, and use various feeding methods to exploit both bound and exposed fluid foods. These mouthpart groups are, in turn, so structurally distinct from each other that they warrant separation into major structural divisions, namely types bearing haustellum-enclosed styli, siphons, labella, and glossae.

Minor patterns tend to be associated with three major themes of major pattern variation, each of which represents a shift in some aspect of food resource use. One theme is the restructuring of mouthparts to capture or process food more efficiently in certain groups. This includes the mortar-and-pestle mechanism in mandibulate hemipteroids used as a second "jaw" for processing solid food, and the rapidly protractile labial mask of odonatan naiads used for securing live prey.

Another prominent theme is the frequent reversion to piercing of biologically contained fluids. Among holometabolous adults, noctuid lepidopterans have converted a siphonate proboscis into a barbed stylet for piercing-and-sucking; cyclorrhaphan dipterans have likewise reverted to "piercing-and-sucking" by modification of the distal labellar surface for piercing dermal tissue; various coleopterans have independently altered typical chewing mouthparts into nonhaustellate piercing structures for feeding on biologically bound fluids. Larval coleopterans and planipennians have separately acquired mandibles for feeding on liquids in live prey. (Notably, this trend is not parallelled in the opposite direction: secondarily mandibulate mouthparts rarely have originated from nonmandibulate mouthparts [see Aldrich (1922) for an exception].)

A third theme is the common acquisition of particle-feeding in diverse mouthpart groundplans. This theme assumes two major ecological trajectories: development of filter-feeding and brush-sweeping for detritivory and microvory by aquatic naiads and larvae, and mouthparts modified for the consumption of terrestrial pollen and spores. The latter trend is represented by the mouthcone of thysanopterans, used to punch-and-suck the contents of pollen. Analogously, coleopterans demonstrate two major types of mouthpart modifications for pollenivory and sporivory. These are the modified penicillate mouthparts of adult forms, used to transport particles to the cibarium where they are either swallowed whole or macerated; and the elongate rostrum of curculionoids, where ratchet-shaped mandibles fragment pollen grains prior to ingestion. Apoid hymenopterans that supplement nectarivory with pollenivory possess well-developed mandibles for extracting pollen.

These three themes--the transformation of the basic biting-and-chewing mouthparts in mandibulate insects into liquid- and particulate feeding--reflect the three fundamental ways that food form is presented to insects. Food occurs as solid matter, as exposed or biologically bound liquid, or as suspended or nonsuspended particles.

CHAPTER 6

THE SAMPLES: A REPRESENTATIVE SELECTION OF INSECT DIVERSITY

6.1. Organization and Coverage of the Data

In this study, a data-entry is defined as a line of mouthpart-morphological and dietary data for a particular examined species, including its number, ordinal abbreviation and Latin binomial name. Data-entry documentation for both mouthpart morphology and diet is provided in Appendix B. In Appendix B, the examined taxa are listed in a phylogenetic scheme, hierarchically by order, suborder (when relevant), superfamily (when relevant), family and finally each genus or genus-and-species, listed alphabetically within its respective family. The classification follows Parker (1982) (see Appendices B and D). Several recently described taxa of new families not included in Parker's encyclopedia were added to Appendix D. Appendix C records the genera and genera-and-species examined as data-entries in the order that they appear in Appendix B.

The data base represents a total familial coverage of 70.0% within the Class Insecta, with a range of familial coverage per order from 25% (Mantodea) to 100%--the latter composed expectedly of mostly the familially small orders of Archaeognatha, Isoptera, Grylloblattodea, Zoraptera and Megaloptera, as well as the more diverse Planipennia and

Mecoptera (Table 4). However, a few large, morphologically diverse orders have familial coverage above the average, namely the Coleoptera (83%), Diptera (90%) and Hymenoptera (78%). The Diptera, containing the most diverse assemblage of mouthpart morphologies of any order, was extensively sampled. The documentation represents adult and immature forms; mouthpart descriptions from the egg and pupal stages have been omitted because of the paucity of source material. Coverage of immatures in the data amounted to a total of 38% of the data base. Larval data originated from both paurometabolous orders with naiad stages, for example Ephemeroptera (93% naiads), Odonata (23% naiads) and Plecoptera (55% naiads) and from holometabolous orders with larval stages, averaging between 25 to 57% larval representation per order (see Table 4 for specifics). Particular attention was paid to diverse families, where sampling was intensified. Diverse families with more than 10 representatives and in decreasing order of abundance are the Carabidae (ground beetles), Staphylinidae (rove beetles), Curculionidae (weevils), Scarabaeidae (scarab beetles), Culicidae (mosquitoes), Formicidae (ants), Hydrophilidae (water scavenger beetles), and Tenebrionidae (darkling beetles). I have attempted to cover as much of insect-mouthpart diversity as the source literature permitted. I focused not only on obvious, major mouthpart morphologies but also on the idiosyncratic--those morphologies, from both immatures and adults, that are rare, specialized, often described in less accessible sources and infrequently discussed in major textbooks or mouthpart review articles.

A percentage representation of the most abundant orders in the data-set is given in Fig. 27. Note that it generally mirrors the

TABLE 4

PERCENTAGE REPRESENTATION OF FAMILIES, SPECIES AND SUBADULT FORMS FOR EACH ORDER IN DATA SET

	Familial representation of orders			*Species representation of the total data set*		*Representation of immature forms (e.g. larvae) per order*	
Order	number of families within the order	number of families represented in data set	percent familial coverage per order	number of species represented in data set	percent of species represented of the total	number of subadult taxa per order in the data set	percent of subadult taxa per order in the data set
Protura	4	2	50.0	3	.22	0	0.0
Collembola	15	8	53.3	8	.59	0	0.0
Diplura	6	2	33.3	3	.22	0	0.0
Archaeognatha	2	2	100.0	3	.22	0	0.0
Thysanura	4	3	75.0	6	.44	0	0.0
Ephemeroptera	19	14	73.7	28	2.05	26	92.9
Odonata	25	8	32.0	22	1.61	6	22.7
Blattodea	5	4	80.0	6	.44	0	0.0
Mantodea	8	2	25.0	4	.29	0	0.0
Isoptera	6	6	100.0	12	.88	0	0.0
Grylloblattodea	1	1	100.0	1	.07	0	0.0
Orthoptera	63	26	41.3	36	2.64	0	0.0
Phasmatodea	11	6	54.5	6	.44	0	0.0
Dermaptera	11	6	54.5	6	.44	0	0.0
Embioptera	8	7	87.5	7	.53	0	0.0
Plecoptera	15	14	93.3	29	2.12	16	55.2
Zoraptera	1	1	100.0	1	.07	0	0.0
Psocoptera	37	10	27.0	12	.88	0	0.0
Anoplura	15	5	33.3	5	.36	0	0.0
Mallophaga	11	10	90.1	16	1.17	0	0.0
Thysanoptera	5	3	60.0	9	.66	0	0.0
Heteroptera	74	55	74.3	70	5.13	1	1.4
Homoptera	55	44	80.0	62	4.54	8	2.9
Megaloptera	2	2	100.0	7	.53	4	7.1
Raphidioptera	2	1	50.0	3	.22	1	33.3
Planipennia	17	17	100.0	32	2.34	15	46.9
Coleoptera	156	130	83.3	347	25.42	171	49.3
Strepsiptera	7	6	85.7	12	.88	5	41.7
Mecoptera	8	8	100.0	16	1.17	4	25.0
Siphonaptera	15	9	60.0	20	1.47	5	25.0
Diptera	123	111	90.2	236	17.29	91	38.6
Trichoptera	39	35	89.7	59	4.32	28	47.5
Lepidoptera	138	72	52.2	141	10.33	73	51.8
Hymenoptera	89	69	77.5	137	10.04	73	53.3
TOTALS:	997	699		1365	100.02	515	
AVERAGES:	70.1%		70.6%				37.7%

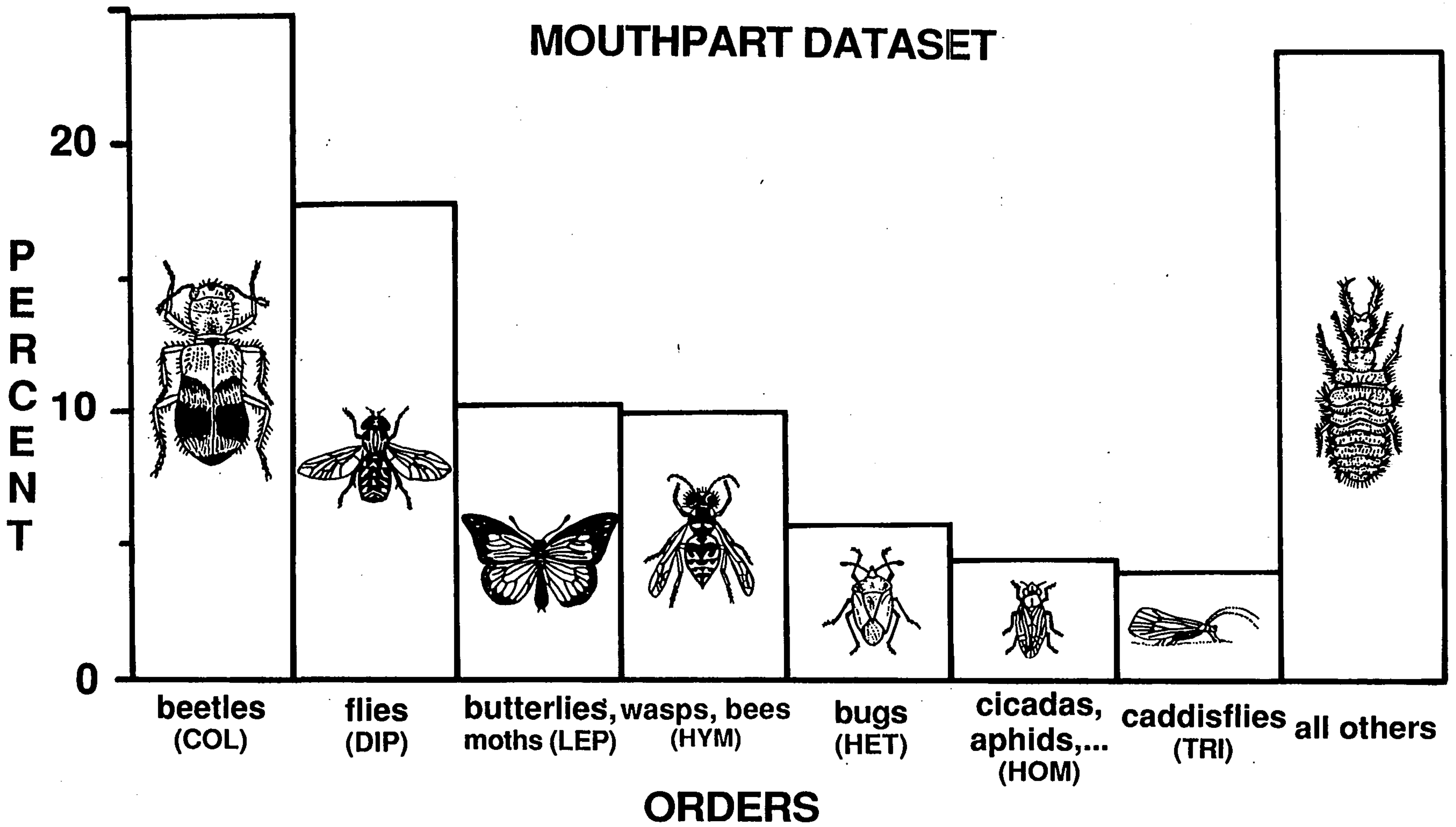


FIGURE 27. Proportional representation of the most abundant hexapod orders in the data set.

proportional diversities of the most diverse orders in the modern hexapod fauna.

6.2. Criteria for Selecting Data

Approximately 1200 mouthpart-morphology references, including journal articles, monographs on the systematics of particular insect taxa, various general accounts, written communication and personal observation, in decreasing order of importance (Appendix B), were used to generate the mouthpart data base (Appendix C). The following criteria were adjudged essential in assessing the quality of the data base.

6.2.1. Data Source Quality

Data sources with line drawings and text descriptions were preferred in assessing character-states of examined species. Sources with photographic documentation or with text descriptions only were less preferable. Sources with idealized abstractions (e.g. DuPorte 1957; Steinmann and Zombori 1981, 1984) were either rejected or on occasion were used only for more generalized (usually head) characters; they were never employed totally for determination of specific details of mouthpart morphology. Generally, monographic sources from the period 1930 to 1970, with line-drawings and head and mouthpart reconstructions, were valued as data sources.

6.2.2. Citation to the Genus or Species Level

Each data source met the requirement of citing the described taxon to either a particular genus, with species indeterminate, or to a particular genus and species. Data describing family-level characters or archetypal reconstructions were not used.

6.2.3. Multiple Data Sources

Whenever possible, multiple data sources were used to assess head and mouthpart characters of an examined taxon. Multiple data sources were used in 72% of all data-entries. The purpose of multiple data sources was to achieve consistency, and when consistency failed, a judgement was made regarding the more reliable data source (or sources) for the examined taxon. Almost always the variation in shape, dimension, or some other morphological attribute of a character occurred within the relatively coarse-grained distinctions established by the character-state categories (Appendix A). On rare occasions, certain genus-level character-states could not be gleaned from the literature, in which case either a blank was left in the data array or the character-state was assessed from relevant morphological or systematic treatments covering a higher taxonomic level (usually the family).

6.2.4. Primary and Secondary Data-Sources

For each examined taxon in Appendix B, a primary data-source (or sources) is indicated by the absence of brackets. Primary data-sources describe the genus or species listed as a data-entry and may refer to either a portion or all of the 49 character-states. Often primary data sources complement each other by describing different morphological regions of the same taxon; occasionally they overlap entirely. When available, secondary data-sources, indicated by brackets, were used to supplement primary data-sources. Thus, secondary data-sources principally fill in the data gaps left by primary sources. Also, brackets were used for those species-resolved data sources-belonging to a different (but always congeneric) species than that of the data entry.

6.3. Summary Statement

This study has sampled as much of the taxonomic breadth of insects as can reasonably be achieved without intensively examining all the monographic literature. An attempt has been made to sample those groups that are taxonomically diverse or exhibit considerable variation in mouthpart structure. Particular emphases have been placed on consulting reference sources that yield reliable descriptive data either at the genus or species level. These and other features are designed to insure quality control in the documentary data that has entered the data-set.

CHAPTER 7

CLUSTERING METHODOLOGY

In this chapter I will (i) discuss the rationale for using a cluster analysis in the evaluation of the data in Appendix C, (ii) describe the algorithms used in the cluster analysis and (iii) assess how the clusters were converted into a classification system of mouthpart types.

7.1. Appropriateness of Cluster Analysis.

Of the several available multivariate techniques for determining pattern within large data-sets, cluster analysis presents three major advantages. First, cluster analysis is a recommended exploratory technique for initially assessing data-set structure. It produces a dendrogram that displays nonoverlapping groupings that are distinct from other such groupings, so that gross patterns can be readily determined. Secondly, cluster analysis is an ideal classificatory technique that partitions a patterned data-set into hierarchical categories that are readily interpretable. Cluster analysis forms clusters by grouping them sequentially, such that each OTU is amalgamated one at a time with another OTU or pre-existing cluster. Thus, a hierarchy of clusters permits a classification based on successively increasing or decreasing inclusivity of OTU's or clusters (Sneath and Sokal 1973). Also, since the produced clusters do not share common elements, each cluster is distinct. Thirdly, cluster analysis is applicable to large data-sets and graphically represents data-set patterns that are readily interpretable by using several criteria. These three features--a proven exploratory technique, appropriateness for generating a phenetic classification and amenability for use in large data-sets--were considered in my choice of cluster analysis.

7.2. Similarity Index

The analysis of the data-set in this study presented three major problems in using conventionally available clus tering programs. The first difficulty was the presence of unordered, multistate, qualitative data which did not permit use of similarity algorithms available on most cluster ana lysis programs installed on mainframe computers. These programs, such as BMDP, SAS and SPSS, are designed for either continuous, quantitative data or, for binarily coded qualitative data. It could have been possible to recode multistate data in the mouthpart data-set binarily. However, this would have produced a huge, unwieldy data-set and incurred the danger of preferentially weighting characters with numerous character-states. If an inappropriate similarity index was used, it would have circumvented my discretionary choice of variables schematically detailed in Fig. 2 and listed in Appendix A. A second limitation of mainframe cluster analysis packages is that in those programs where multistate data is accepted, such as Block Clustering on BMDP3M, there is an absolute limit of nine character-states per character, thus disallowing 16 of my 49 variables (Appendix A). Recoding these variables would introduce the data-set biases mentioned above. Finally, the relevant cluster analysis programs do not accept cases with missing data; if missing data are present, the cases are rejected from the analysis.

Given these limitations, a FORTRAN program was written to produce a 1365 X 1365 Jaccard similarity matrix of cases (taxa in Appendices B and C). The Jaccard index of similarity was used because it is a simple, easily understood metric that measures the proportion of identical character-states in a pair of OTU's. The Jaccard index (S_j) places the number of positive matches among characters between two cases over the number of matches and mismatches, where A is the number of matches and B the number of mismatches, calculated for any two cases on the 49 characters (Sneath and Sokal 1973):

$$S_j = \frac{A}{A + B},$$

Note that negative matches are excluded (and actually irrelevant given the coding scheme employed) and that the numerator equals the number of characters (49), except when missing data are encountered.

This matrix was then imput into program BMDP1M for cluster analysis. The choice of BMDP1M program, *Cluster Analysis of Variables* (Hartigan 1988), was made since it will accept a large external similarity matrix as input and perform simple, unweighted pair-group clustering upon it. Consequently the BMDP1M program was used to cluster cases (OTU's), even though they were outputted technically as "variables." The advantage of this two-step process is that the three major objections for using similarity indices provided by mainframe cluster analysis programs were circumvented. The Jaccard index of similarity was used because of all the available similarity measures, it was the only commonly used measure appropriate for the unordered, multistate, qualitative data of my data-set. The Jaccard algorithm (S_j) places the number of positive matches of all characters on two data-set cases over the number of matches and mismatches (Sneath and Sokal 1973). Negative matches were not relevant because of the coding scheme employed, and matches based on joint presence of missing data were excluded from the analysis. Thus, where A is the number of matches and B the number of mismatches, a similarity index was calculated for any two cases on the 49 characters. The Jaccard algorithm enters only those character-states in common between two cases and ignores all other matches and mismatches in the numerator. The advantage of the Jaccard algorithm is that the derived similarity matrix is based only on mutual presence of nonzero characters and hence is a conservative yet realistic index of similarity

7.3. Clustering Algorithm

The unweighted average linkage algorithm of joining clusters was used in the analysis. Average linkage is calculated after each clustering cycle as the mean similarity between all members of a newly formed cluster and members of other previous clusters (see Dillon and Goldstein 1984). Consequently, average linkage is the summation of similarity values, *s*, between OTU_i of cluster i and OTU_j of cluster j, divided by the product of the number of OTU's of the two clusters ($n_i n_j$):

$$D_{al} = \frac{\sum\sum_{ij} \underline{s}_{ij}}{n_i n_j}.$$

The advantage of average linkage is that it de-emphasizes the extreme distance values of cluster outliers that are present in single linkage. Thus, there is a greater tendency for clusters to be formed homogeneously, resulting in minimization of group outliers ("chaining") in the resulting dendrogram.

7.4. Interpretation of the Dendrogram

Several somewhat subjective methods are used for defining groups in the dendrogram produced by the cluster analysis. Commonly cited criteria are (i) evaluation of subcluster discreteness by reference to branch lengths, (ii) overall dendrogram topology as a guide to subcluster separation (b) evaluation of cluster branch-lengths, (iii) levels of similarity and (iv) absence of chaining, corresponding to breaks in the data. I generally avoided use of a "phenon line," particularly since the number of members in otherwise discrete clusters varied by at least three orders of magnitude (cf. mouthpart classes 3 and 32 in Table 5), and the basal branches of diverse clusters appeared to be at a lower amalgamation level than those of nondiverse clusters.

In addition to the dendrogram-specific criteria above, the resulting clusters must also meet several biologically-based criteria. These criteria include (i) the demonstration that the clusters are internally rationalizable in terms of a common mouthpart structure, (ii) determination of structural uniqueness of the mouthpart characters when compared to other clusters of the dendrogram and (iii) coincidence with a mouthpart morphology previously recognized in the literature, when possible. In about 90% of the cases, the first two criteria, in addition to dendrogram topology, were sufficient to warrant designation of particular clusters as distinct mouthpart types. In a few instances, the last criterion was also important in making a final determination. Neither taxonomic abundance nor diversity was used in the evaluation of clusters.

Taxon membership within the cluster must be recognizable in terms of a consistent theme of mouthpart structure. For making meaningful assignments, both primary and secondary clusters must exhibit an identifiable, key structural feature or ensemble of features shared by all cluster members, from which the group derives its name (see Section 8.2.). Two potential difficulties in this regard are intergrading taxa between major clusters, which appears to be minimal, and extremely large clusters which contain a significant amount of chaining in the subclustering taxa. The later point confounds class discrimination and the use of phenon lines. The vast adult-ectognathate class (Figs. 28, 36a-g; Table 5) is the best example of this: it can be partitioned into two subclusters, each of which may be rationalized based on clustering pattern but not on mouthpart structure.

The second biologically-based criterion is structural uniqueness of the represented mouthparts in a particular cluster with respect to other such clusters. Not only must clusters be internally consistent, sharing common mouthpart elements, but each cluster must clearly correspond to an anatomical structure that is differentiated from other clusters. Thus, a few isolated taxa were not assignable and are considered anomalous. (They are discused under "Structural Themes" in the appropriate sections of Chapter 8.)

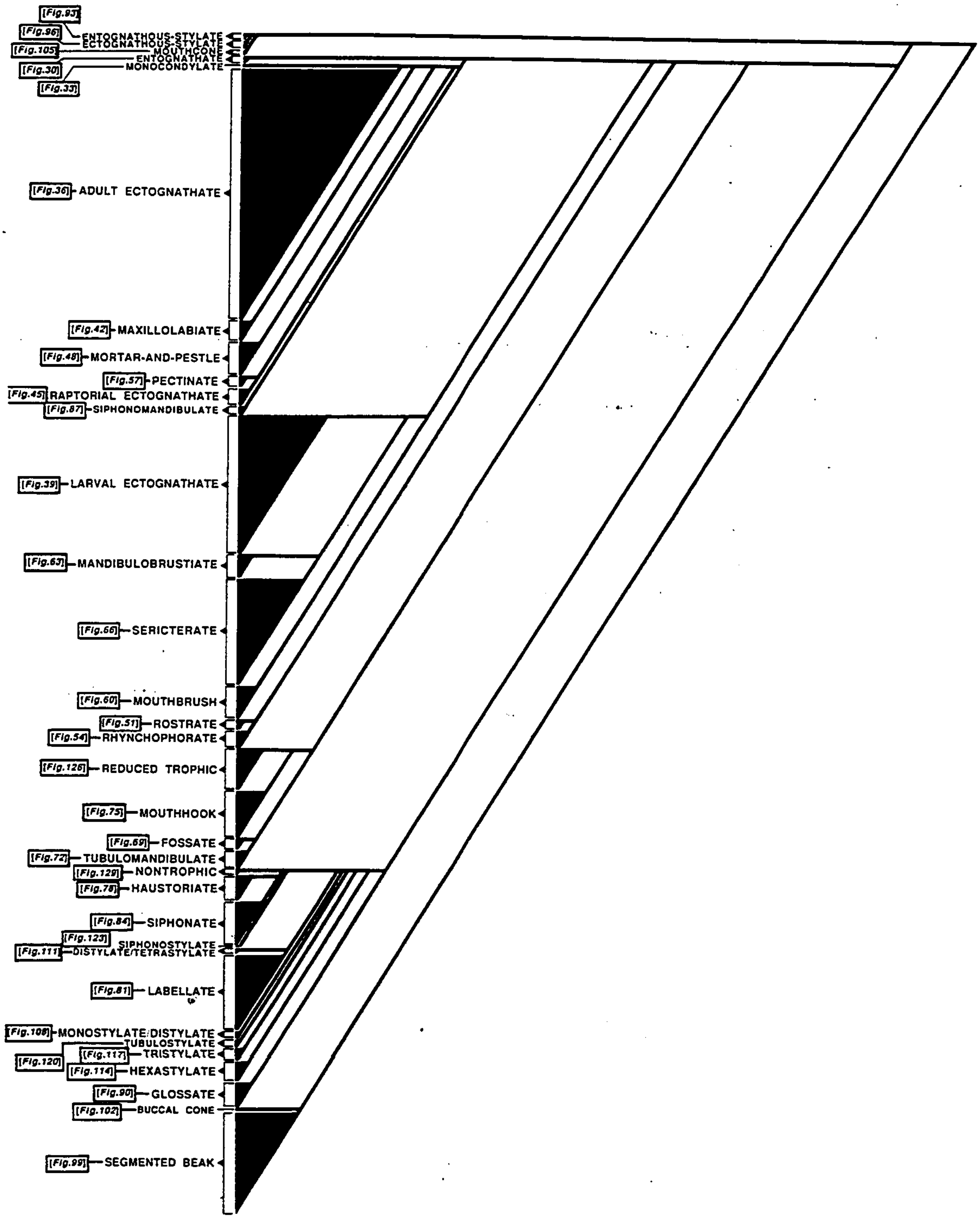


FIGURE 28. Cluster analysis dendrogram of Recent hexapod mouthparts. See text for methods of data analysis used for the generation of this dendrogram.

TABLE 5

A MORPHOLOGICAL CLASSIFICATION OF RECENT HEXAPOD MOUTHPARTS

mouthpart series	*no.*	*mouthpart class*	*included taxa**	*life stage*	*number studied*
MANDIBULATE	1.	**Entognathate**	Collembola, Diplura	nymphs, adults	10
	2.	**Monocondylate**	Archaeognatha	nymphs, adults	3
	3.	**Adult-Ectognathate**	Thysanura, Blattodea, Mantodea, Phasmatodea, Grylloblattodea, Orthoptera, Isoptera, Dermaptera, Embioptera, Plecoptera, Zoraptera, Megaloptera, Planipennia, Megaloptera, Raphidioptera, Coleoptera, Lepidoptera (Zeugloptera), Hymenoptera (Symphyta, Apocrita-Parasitica)	adults, naiads of Plecoptera, a few larvae	291
	4.	**Larval-Ectognathate**	Coleoptera, Mecoptera, Siphonaptera, Diptera (Anisopodidae), ?Trichoptera (Phryganopsychidae), Lepidoptera (Zeugloptera)	larvae	164
	5.	**Maxillolabiate**	Hymenoptera (Apocrita)	adults	24
	6.	**Raptorial-Ectognathate**	Odonata	adults	22
	7.	**Mortar-and-Pestle**	Psocoptera, Mallophaga (Amblycera, Ishnocera)	nymphs, adults	27
	8.	**Rostrate**	Mecoptera; Planipennia (Nemopteridae)	adults	13
	9.	**Rhynchophorate**	Coleoptera (Curculionoidea)	adults	18
	10.	**Pectinate**	Ephemeroptera	naiads	26
	11.	**Mouthbrush**	Diptera (Nematocera); Coleoptera (Buprestidae); Lepidoptera (Phyllocnistidae, Gracillariidae)	larvae	3
	12.	**Mandibulo-brustiate**	Trichoptera	larvae	28
	13.	**Sericterate**	Lepidoptera (Glossata); Hymenoptera	larvae	125

TABLE 5 (Continued)

mothpart series	no.	mouthpart class	included taxa*	life stages	number studied
MANDIBULO-CANALICULATE	14.	Fossate Complex	Planipennia	larvae	15
	15.	Tubulo-mandibulate	Coleoptera (Hygrobiidae, Dytiscidae, Gyrinidae, Haliplidae, Lampyridae, ?Telegeusidae, Drilidae, Lycidae, Phenogodidae, Cantharidae, Brachypsectridae, Omethidae)	larvae	20
	16.	Mouthhook	Diptera (Cecidomyiidae, Brachycera)	larvae	55
LABELLATE	17.	Haustoriate	Trichoptera	adults	30
	18.	Labellate	Diptera (Tipuloidea, Tanyderidae, Ptychopteridae, Bibionoidea, Brachycera); Mecoptera (Nannochoristidae)	adults	5
SIPHONATE	19.	Siphonate	Lepidoptera (Glossata)	adults	53
	20.	Siphono-mandibulate	Coleoptera (?Hydrophilidae, Meloidae, Rhipiphoridae)	adults	5
GLOSSATE	21.	Glossate	Planipennia (Nemopteridae); Hymenoptera (?Torymidae, Sapygidae, Scolioidea, Vespoidea, Sphecoidea, Apoidea)	adults	29
STYLATE-NON-HAUSTELLATE	22.	Entognathous-Stylate	Protura; Collembola (Neanuridae)	nymphs, adults	4
	23.	Ectognathous-Stylate	Orthoptera (Cooloolidae); Coleoptera (Sphaeridae, Rhysodidae, Leiodidae, Cerylonidae, Corylophidae, Eucinetidae)	adults, a larva	13
STYLATE-HAUSTELLATE	24.	Segmented Beak	Homoptera, Heteroptera	nymphs, adults	118
	25.	Buccal Cone	Anoplura; Mallophaga (Haematomyzidae)	nymphs, adults	6

TABLE 5 (Continued)

mouthpart series	no.	mouthpart class	included taxa*	life stages	number studied
STYLATE-HAUSTELLATE (Continued)	26.	Mouthcone	Thysanoptera	nymphs, adults	9
	27.	Monostylate/ Distylate	Diptera (Asilidae, Acroceridae, Empididae, Bombyliidae)	adults	8
	28.	Distylate/ Tetrastylate	Diptera (Anisopodidae, Rhagionidae, Mydidae, Therevidae, Ironomyiidae)	adults	9
	29.	Hexastylate	Diptera (Nematocera, Tabanoidea)	adults	27
	30.	Tristylate	Siphonaptera	adults	15
	31.	Tubulostylate	Diptera (Glossinidae, Hippoboscidae, Streblidae, Nycteribidae)	adults	10
	32.	Siphonostylate	Lepidpotera (Noctuidae)	adults	2
AGNATHATE	33.	Reduced-Trophic	Homoptera (Neococcoidea); Coleoptera (Eucnemidae, Rhipiphoridae); Strepsiptera; Diptera (Nymphiomyidae, Hyperoscleidae, Gasterophilidae, Acroceridae); Lepidoptera (Zygaenoidea); Hymenoptera (Apocrita: Parasitica)	nymphs larvae, adults	52
	34.	Nontrophic	Ephemeroptera; Lepidoptera (Hepialoidea, Lasiocampidae, Saturniidae)	adults	9

Notes

*Included taxa are listed as orders and, when relevant, suborders superfamilies, or families of orders possessing members in the given mouthpart class. Not every ordinal or subordinal grouping necessarily contains members only in the stated mouthpart class. For example, whereas most coleopteran larvae are larval ectognathate (Class 4), others are tubulomandibulate (Class 15) or reduced mandibulate (Class 33).

Lastly, an important but not necessarily requisite criterion was the identification of a particular cluster with a previously documented mouthpart type from the literature. If the above criteria were equivocal regarding the uniqueness of a given cluster, corroboration from the literature, or lack thereof, was sought to lend credence to a final decision.

CHAPTER 8

RESULTS AND INTERPRETATION

In this section I will first present a cursory historical survey of attempts to understand the diverse repertoire of insect mouthparts, focusing on major conceptual changes as well as standard (usually textbook or review article) treatments of mouthpart form and diversity. Then I will explain those criteria by which primary and secondary mouthpart groupings are established from the data-set. Finally, I will treat the derived mouthpart groups formally. In my formal treatment of each mouthpart group I will (i) describe their structural features, (ii) cite key phenocharacters, (iii) discuss taxonomic representation and ecological roles, (iv) evaluate structural themes within the mouthpart class, (v) discuss geochronologic range and fossil history, (vi) mention previous recognition of the mouthpart class in the literature and (vii) provide a brief review of relevant literature.

8.1. A Brief History of Studies of Mouthpart "Classes"

8.1.1. Aristotle

Aristotle (384-322 B.C.) recognized at least four major mouthpart types of insects in his works on natural history. He described forms with biting mandibles, a lapping "tongue," a sponging "tongue," and piercing stylets. He ascribed solid food diets to mandible-bearing insects, saying that "insects such as have teeth [=mandibles] are omnivorous" in his *De Historia Animalium* (Book V, Chap. 11, line no. 596b). In a rather exhaustive treatment on apiculture, he comments that bees feed on "... the juices of the flowers ... with the organ that resembles a tongue" (*Historia Animalium*, V, 22: 554a). As for certain flies, he observes that some flies possess a "tongue" with a"... spongy texture fit to absorb nutriment" (*De Partibus Animalium*, IV, 6: 683a). In a short discourse on the cicada, Aristotle notes that "... the mouth and the tongue are united so as to form a single part, through which, as though a root, the insect sucks up fluids on which it lives" (*De Partibus Animalium*, IV, 5: 682a). In Aristotle's discussion, there are two major categories of mouthparts: those with "teeth" (i.e. mandibles) and those without teeth, having a proboscis. Of the latter, three subcategories were recognized, namely (i) those feeding on all saps, such as the sponging mouthparts of flies, (ii) the blood-sucking, stylate mouthparts of mosquitoes and (iii) those feeding on sweet sap, particularly glossate bees. Aristotle combined empirical observation with inference in his exposition on mouthparts, often suggesting causal relationships between structure and diet. He was well aware of the scope of insect-mouthpart variation:

> The parts concerned in nutrition are not alike in all insects, but show considerable diversity (*De Partibus Animalium*, IV, 5: 682a).

The morphological and functional insight of Aristotle was not surpassed until the invention of the microscope during the late 1500's. Although some detailed illustrations of microscopic mouthparts were made by Hooke (1667), it was not until the late 1700's and early 1800's that natural philosophers attempted to understand mouthpart form.

8.1.2. The Impact of Fabricius

By the time of Fabricius (1745-1808) comparative morphology was already a well-established field. However, unlike previous and penecontemporaneous natural philosophers, Fabricius emphasized mouthpart structure in taxonomically categorizing insects and other arthropods (Tuxen 1967). He divided all insects into "*Kerfe mit bei[ss]enden Mundtheilen*" and "*Kerfe mit saugenden Mundtheilen* (Burmeister 1832: 667). The former group, mandibulates, in turn was divided into a group bearing four or six palpi and a group bearing only two palpi. Forms with sucking mouthparts were divided into proboscate forms with a spiral "tongue" (lepidopterans), forms with a filtering proboscis (some hemipterans) and stylus-bearing forms (his "setae," dipterans). Later, in 1799, though retaining the fundamental division between mandibulate and sucking mouthparts, he modified his earlier classification by including the arachnid chelicerae, crustacean maxillipeds and other arthropodan mouthpart structures in his classification.

While Linneaus singularly emphasized wings and Fabricius did likewise for mouthparts as basic characters in their insect taxonomies, such approaches were often considered biased (Lindroth 1973). J.A. Scopoli, for example, cautioned against exclusive use of particular structures or structural regions, stating that:

> Classes [et] genera naturalia non sola instrumenta ciburia, non solae alae, nec solae antennae constituunt, sed structura totius ac cuiusque vel minimi discriminis diligentissima observatio (Scopoli 1777: 401).

This was a general criticism of Fabricius' (1775) classification of insects. However, in a response to an intellectual disciple of

Scopoli, P.A. Latreille (1762- 1833), Fabricius proclaimed: "mixta semper chaos praebent," maintaining his use of mouthparts as essential to insect classification (Lindroth 1973). Later, Savigny demonstrated that all major mouthpart elements of insects are fundamentally homologous (Richards 1973), thus lending credence to Fabricius' system of classification.

Fabricius' influence on mouthpart structure continued in classificatory systems established by other entomologists. It was reflected in the formal terms, "Mandibulata" and "Haustellata" of the quinary system of MacLeay (1821) and the influential system of Kirby and Spence (1826). By contrast, Latreille's (1832) classification integrated mouthpart structure, wings and metamorphosis, of which metamorphosis was considered as fundamental by Burmeister in the early 1830's (Lindroth 1973). (All three features are used as high-level taxonomic characters to this day.) Attempts by Fabricius to use mouthparts at lower taxonomic scales--especially the generic level--proved futile because of their frequent structural similarity in otherwise structurally diverse genera (Tuxen 1967). Nevertheless, his insight proved refreshingly modern:

> The mouthparts in insects differ to a high degree and it is reasonable that they mark the most natural genera, since these parts must be built up according to the nourishment of every insect, and their whole biology is dependent on their nourishment . . .
>
> Those whose nourishment and biology are the same, must then also belong to the same genus (Fabricius 1790: 214; translated from the Danish by Tuxen [1967]).

Eventually mouthparts became supplanted not only by other major structural characters, especially wings and type of metamorphosis, but also features such as tarsal formulae and ovipositor structure (for example, see ordinal diagnoses given by Richards and Davis [1977]). This shift occurred during the mid-1800's and was already evident in Burmeister's influential *Handbuch der Entomologie* (1832), wherein more recent classificatory systems pursued integrated approaches.

8.1.3. Metcalf and Recent Contributions

A hiatus in the systematization of mouthpart form occurred for almost a century. When mouthparts were mentioned, they were either adjunct to taxonomic studies or they were purely descriptive accounts of particular, often economically important species. However, in 1929 Metcalf classified insect mouthparts, focusing on their modes of action and general role in crop destruction. Although his primary-level classification was based on functional groupings, secondary-level groupings corresponded closely to taxonomic groupings. In a 1962 revision of this classification, a few groupings were added, although the basic outline of mouthpart structure remained intact. The perspective of Metcalf and (1929) Metcalf et al. (1962) was a valuable one, since it removed mouthpart structure from the realm of phylogenetically related groupings (see Table 6). They established not only that mouthpart structure need not be necessarily related to any phylogenetic concepts but, more importantly, contributed insight into the role of mouthpart structure, feeding and diet. Thus, the integration of mouthpart structure and function, and aspects of feeding and diet, was a valuable prerequisite for understanding insect/environmental interactions independent of phylogenetically-based taxonomic membership.

TABLE 6

HISTORY OF HEXAPOD MOUTHPART NOMENCLATURE

<table>
<tr><th rowspan="2"><i>author</i></th><th rowspan="2"><i>basis of classification</i></th><th colspan="6"><i>classification:</i></th></tr>
<tr><th>1</th><th>2</th><th>3</th><th>4</th><th>5</th><th>6</th></tr>
<tr><td>Labandeira 1990 (this study)</td><td>Morphological</td><td>MANDIBULATE: entognathate</td><td>MANDIBULATE: monocondylate</td><td>MANDIBULATE: adult ectognathate</td><td>MANDIBULATE: larval ectognathate</td><td>MANDIBULATE: maxillo-labiate</td><td>MANDIBULATE: raptorial ectognathate</td></tr>
<tr><td>Clairville 1798-1806; Stephens 1828</td><td>morphological; used as a formal taxon</td><td>▨</td><td>▨</td><td colspan="4">MANDIBULATA</td></tr>
<tr><td>Metcalf 1929</td><td>Mixed: higher level morphological; middle level functional; lower level, when present, taxonomic</td><td>▨ ? ▨</td><td>▨ ? ▨</td><td colspan="4">MANDIBULATE SERIES:
chewing type</td></tr>
<tr><td>Metcalf, Flint & Metcalf 1962</td><td>Mixed: functional at higher level; functional or lower level</td><td colspan="6">CHEWING TYPE
[grinding or masticatory subtype;
grasping or predaceous subtype;
brushing, spatulate or scraping subtype]</td></tr>
<tr><td>James & Harwood 1969</td><td>Mixed: higher level taxonomic (defined functionally), lower level morphological & functional</td><td>▨</td><td>▨</td><td colspan="4">ORTHOPTERAN TYPE:
(biting and chewing)</td></tr>
<tr><td>Denis & Bitsch 1973</td><td>Mixed: functional at higher level; lower level morphol. & taxonomic</td><td>▨</td><td colspan="5">APPAREIL BUCCAL BROYEUR</td></tr>
<tr><td>Borror, DeLong & Triplehorn 1976</td><td>Mixed: morphological at higher level; taxonomic at lower level</td><td>▨</td><td>▨</td><td>MANDIBULATE</td><td>▨</td><td colspan="2">MANDIBULATE</td></tr>
<tr><td>Ross, Ross & Ross 1982</td><td>Functional</td><td colspan="6">CHEWING TYPE</td></tr>
<tr><td>Chaudonneret 1982-1989</td><td>Functional-morphological at higher level; taxonomic at lower level</td><td>PIECES BUCCALES BROYEUSES ENTOTROPHES</td><td colspan="3">PIECES BUCCALES BROYEUSES: Theme</td><td>▨</td><td>PIECES BUCCALES PREDATRICES LABIALES: Cas de larves d'Odonates</td></tr>
<tr><td>Smith 1985</td><td>Functional</td><td colspan="6">CUTTING AND CHEWING</td></tr>
</table>

TABLE 6 (Continued)

classification								
7	8	9	10	11	12	13	14	15
MANDIBULATE: mortar-and-pestle	MANDIBULATE: rostrate	MANDIBULATE: rhynchophorate	MANDIBULATE: pectinate	MANDIBULATE: mouthbrush	MANDIBULATE: mandibulo-brustiate	MANDIBULATE: sericterate	MANDIBULO-CANALICULATE: fossate complex	MANDIBULO-CANALICULATE: tubulomandibulate
MANDIBULATA			\\\\\\\\\\\	\\\\\\\\\\\	MANDIBULATA			
MANDIBULATE SERIES chewing type			\\\\\\\\\\\	\\\\\\\\\\\	MANDIBULATE SERIES: chewing type		MANDIBULATE SERIES: predatory type	
CHEWING TYPE chewing or masticatory subtype			\\\\\\\\\\\	CHEWING TYPE: brushing, spatulate, or scraping subtype	DEGENERATE TYPE: hymenopterous, trichopterous and lepidopterous subtype		CHEWING TYPE: grasping-sucking or mandibulo-suctorial subtype	
ORTHOPTERAN TYPE: biting and chewing			\\\\\\\\\\\	mosquito and blackfly feeding apparatus	\\\\\\\\\\\	\\\\\\\\\\\	\\\\\\\\\\\	\\\\\\\\\\\
APPAREIL BUCCAL BROYEUR:	"la partie anterieure de la tete s'allonge en un rostre"		EPHEMERES: larves	\\\\\\\\\\\	APPAREIL BUCCAL BROYEUR: larves de Trichopteres et Lepidopteres.		APPAREIL BUCCAL PIQUEUR-SUCCEUR:paire de crochets	APPAREIL BUCCAL PIQUEUR-SUCCEUR: mandibules canal
MANDIBULATE							"CHEWING-SUCKING"	
CHEWING TYPE			FILTERING TYPE		CHEWING TYPE	●	\\\\\\\\\\\	\\\\\\\\\\\
\\\\\\\\\\\	PIECES BUCCALES DE TYPE BROYEUR: Cas de la Panorpe	PIECES BUCCALES DE TYPE BROYEUR: Cas de la Curculionide	\\\\\\\\\\\	PIECES BUCCALES BROYEUSES ET FILTRANTES	\\\\\\\\\\\	PIECES BUCCALES BROYEUSES: Theme	PIECES BUCCALES PREDATRICES SUCEUSES MANDIBULO-MAXILLAIRES: Cas des larves de Planipennes	PIECES BUCCALES PREDATRICES SUCEUSES MANDIBULAIRES: Cas des larve de quelques Coleopteres
\\\\\ ? \\\\	CHEWING AND CUTTING		FILTER-FEEDING		FILTER FEEDING: net spinners--caddis flies	CUTTING AND CHEWING	PIERCING-AND-SUCKING	

TABLE 6 (Continued)

author	classification							
	16	17	18	19	20	21	22	23
Labandeira 1990 (this study)	MANDIBULO-CANALICULATE mouthhook	LABELLATE: haustoriate	LABELLATE: labellate	SIPHONATE: siphonate	SIPHONATE: siphono-mandibulate	GLOSSATE: glossate	STYLATE-NON-HAUSTELLATE: entognathous-stylate	STYLATE-NON-HAUSTELLATE: ectognathous-stylate
Clairville 1798-1806	\\\\\\\\\\\	MANDIBULATA	HAUSTELLATA		\\\\\\\\\\\	MANDIBULATA	\\\\\ ? \\\\\	\\\\\ ? \\\\\
Metcalf 1929	\\\\\\\\\\\	\\\\\\\\\\\	HAUSTELLATE SERIES: sponging type	HAUSTELLATE SERIES: siphoning type	\\\\\\\\\\\	HAUSTELLATE SERIES: chewing-lapping type	MANDIBULATE SERIES: acuminate type	\\\\\\\\\\\
Metcalf, Flint & Metcalf 1962	DEGENERATE TYPE: dipterous larvae subtype	\\\\\\\\\\\	SPONGING TYPE	SIPHONING TYPE	\\\\\\\\\\\	CHEWING-LAPPING TYPE	\\\\\\\\\\\	\\\\\\\\\\\
James & Harwood 1969	mouth hooks of cyclorrhaphous Diptera	\\\\\\\\\\\	DIPTERAN TYPE: fourth subtype, the house fly	LEPIDOPTERAN TYPE: suctorial coiled tube	\\\\\\\\\\\	HYMENOPTERAN TYPE: suctorial lapping organ	\\\\\\\\\\\	\\\\\\\\\\\
Denis & Bitsch 1973	\\\\\\\\\\\	APPAREIL BUCCAL LECHEUR-SUCEUR			APPAREIL BUCCAL LECHEUR-SUCEUR: Meloidae	APPAREIL BUCCAL LECHEUR-SUCEUR	APPAREIL BUCCAL LECHEUR-SUCEUR: certaines larves de Coleopteres (Dytiscidae, Gyrinidae, Lampyridae)	
Borror, DeLong & Triplehorn 1976	\\\\\\\\\\\	\\\\\\\\\\\	HAUSTELLATE: mouthparts of higher Diptera with sponging	HAUSTELLATE mouthparts of Lepidoptera	\\\\\\\\\\\	"CHEWING-SUCKING"	\\\\\\\\\\\	\\\\\\\\\\\
Ross, Ross & Ross 1982	\\\\\\\\\\\	\\\\\\\\\\\	SPONGING TYPE	SIPHONING TUBE TYPE	\\\\\\\\\\\	CHEWING-LAPPING TYPE	\\\\\\\\\\\	\\\\\\\\\\\
Chaudonneret 1982-1989	REDUCTION DES PIECES BUCCALES DE TYPE BROYEUR: Cas de larves des Dipteres	PIECES BUCCALES LECHEUSES: La trompe des Phryganes	PIECES BUCCALES LECHEUSES: L'appareil lecheur de quelques Dipteres	PIECES BUCCALES LECHEUSES: La spiritrompe des Papillons	PIECES BUCCALES BROYEUSES-LECHEUSES: Trompe lecheuse maxillaire	PIECES BUCCALES BROYEUSES-LECHEUSES: Cas de Hymenopteres	PIECES BUCCALES BROYEUSES ENTOTROPHES	PIECES BUCCALES PICQUEUSES: Coleopteres adultes
Smith 1985	\\\\\\\\\\\	FEEDING ON FREE LIQUIDS					\\\\\\\\\\\	\\\\\\\\\\\

TABLE 6 (Continued)

classification							
24	25	26	27	28	29	30	31
STYLATE-HAUSTELLATE: segmented beak	STYLATE-HAUSTELLATE buccal cone	STYLATE-HAUSTELLATE: mouthcone	STYLATE-HAUSTELLATE: monostylate/ distylate	STYLATE-HAUSTELLATE: distylate/ tetrastylate	STYLATE-HAUSTELLATE: hexastylate	STYLATE-HAUSTELLATE: tristylate	STYLATE-HAUSTELLATE: tubulostylate
HAUSTELLATA							
HAUSTELLATE SERIES: piercing-sucking type (hemipterous subtype]	HAUSTELLATE SERIES: piercing-sucking type [anoplurous subtype]		▨	HAUSTELLATE SERIES: piercing-sucking type [common biting fly or dipterous subtype]		HAUSTELLATE SERIES: piercing-sucking type [flea or siphonapterous subtype]	▨
PIERCING-SUCKING TYPE: bug or hemipterous subtype	PIERCING-SUCKING TYPE: [louse or anoplurous subtype]		▨	HAUSTELLATE SERIES: piercing-sucking type [common biting fly, or dipterous subtype]		PIERCING-SUCKING TYPE: flea or siphonapterous subtype	▨
HEMIPTERAN TYPE: piercing-sucking	ANOPLURAN TYPE: piercing-sucking subtype (the stable fly)		▨	DIPTERAN TYPE: second subtype, the horse fly, and third subtype, the stable fly	DIPTERAN TYPE: first subtype, the mosquito	SIPHONAPTERAN TYPE: piercing-sucking	DIPTERAN TYPE: fifth subtype the sheep ked
APPAREIL BUCCAL LECHEUR-SUCEUR							▨
HAUSTELLATE: mouthparts of Hemiptera and Homoptera	HAUSTELLATE: mouthparts of sucking lice		HAUSTELLATE: mouthparts of robber flies	HAUSTELLATE: mouthparts of biting lower Diptera		HAUSTELLATE: mouthparts of fleas	▨
PIERCING-SUCKING TYPE							▨
▨	PIECES BUCCALES PICQUEUSES: Anoploures	PIECES BUCCALES PICQUEUSES: Thysanopteres	PIECES BUCCALES PICQUEUSES: Dipteres picqueurs: Cas de Asilides	▨	PIECES BUCCALES PICQUEUSES: Dipteres picqueurs: Cas de Tabanides	PIECES BUCCALES PICQUEUSES: Aphanipteres	▨
PIERCING-AND-SUCKING							

TABLE 6 (Continued)

author	*classification* 32	 33	 34
Labandeira 1990 (this study)	STYLATE-HAUSTELLATE: siphonostylate	AGNATHATE: reduced trophic	AGNATHATE: nontrophic
Clairville 1798-1806	▨	▨	▨
Metcalf 1929	▨	▨	▨
Metcalf, Flint & Metcalf 1962	▨	▨	▨
James & Harwood 1969	▨	▨	▨
Denis & Bitsch 1973	▨	REDUCTION DES PIECES BUCCALES	REDUCTION DES PIECES BUCCALES
Borror, DeLong & Triplehorn 1976	▨	▨	▨
Ross, Ross & Ross 1982	▨	▨	▨
Chaudonneret 1982-1989	PIECES BUCCALES LECHEUSES: La spiritrompe des Papilions: "certaines Noctuelles tropicales"	REDUCTION DES PIECES BUCCALES DE TYPE BROYEUR: Cas de males de Chenilles, Strepsipteres	REDUCTION DES PIECES BUCCALES DE TYPE BROYEUR: Cas de Ephemeropteres Strepsipteres; Ephemeropteres
Smith 1985	PIERCING -AND- SUCKING	▨	▨

R.E. Snodgrass published in the *Smithsonian Miscellaneous Collections* several major synopses of insect mouthpart structure, illustrating the variations of particular functional themes. He often devoted lengthly articles to the mouthpart structure, for example, of biting and sucking insects of medical importance, fleas, mandibulate arthropods, and more specialized accounts of particular insects such as dragonfly larvae, mosquitoes and the honey bee (Snodgrass 1928, 1932, 1935, 1943, 1944, 1950). More recently, comprehensive reviews by Matsuda (1965), Denis and Bitsch (1973) and Chaudonneret (1982-1989) have presented a summary of major studies of mouthpart structure, presented by taxonomic order. These reviews are predominantly descriptive, focusing more on musculature than Snodgrass did. This trend was altered by Smith (1985), who, while not attempting a taxonomically comprehensive survey, nevertheless inventoried much of the recent functional-morphology literature. He discussed the mechanisms of operation of several often taxonomically convergent mouthpart types as functionally unique ways to secure particular foods.

8.1.4. The Confounding of Structural, Functional and Taxonomic Terms

The history of the recognition of mouthpart groupings has been laden with use of three distinct types of terms: structural terms, functional terms and taxonomic terms. These terms have often been employed in a confusing manner. Frequently they substitute indiscriminantly for each other, such as purely descriptive, structural terms substituting for process-related terms that describe the action of mouthparts, or vice-versa. Also, formal taxonomic terms, or their common-name synonyms, have been used to characterize adjectively particular mouthpart types. Aristotle used a structural basis for his primary divisions of mouthpart type (e.g. "having teeth" versus "having a proboscis;" but separated his second level proboscate forms by using functional statements regarding the mode of feeding (Monge 1973). Fabricius (1775, 1799) used only structural terms for all of his three hierarchical levels of mouthpart structure. However, MacLeay (1819-1821), Kirby and Spence (1826) and Stephens (1828) elevated the common designations of mandibulate and haustellate, to formal, supraordinal taxonomic designations--"Mandibulata" and "Haustellata"--to which various insect orders were assigned. Latreille (1832), by contrast, devised an eclectic system of using many kinds of insect features, using mouthpart type as a sixth-level distinction in his dichotomous keys.

This muddling of terms has continued to the present day (Table 6). For example, the butterfly proboscis has been termed and classified as (i) a "lepidopteran-type" mouthpart by James and Harwood (1969), a taxonomic term, or as (ii) a "siphoning tube" by Ross et al. (1982), a functional statement, and as (iii) a "haustellate" type of mouthpart by Borror et al. (1976), a structural descriptor. As will be shown, there is considerable mouthpart convergence taxonomically, and since the same functional process can be performed by more than one structural mouthpart type (or vice-versa), this confusion has obscured the nominally clear distinctions that should be made among mouthpart structure, mouthpart function and taxa of a given mouthpart class. For this reason, I have based my classification of mouthparts as much as possible on structural criteria (Sections 4.4, 5.1). I consider ecologically-based functional-feeding-groups (Cummins and Merritt 1984) and taxonomic membership as expressions that generally do not correspond directly to particular structurally-based mouthpart groupings.

It is in this context that I propose a standardization of terminology for designating various projecting, food-reaching mouthpart organs of the insect head (Table 7). Although historically some of these proposed terms have been applied to particular insect mouthpart ensembles and have been used with some degree of constancy, many have not. Confusion should be eliminated regarding general names that are used indiscriminately to refer to various insect trophic organs among several major insect clades, and specific terms restricted to the trophic organs of narrowly-defined clades.

The more important emendations are the following: (i) that the term proboscis be restricted to the mouthparts of dipterans and siphonapterans; (ii) that mecopteran and convergent mouthparts be designated as a *rostrum* and curculionoid mouthparts be considered a *snout*; (iii) that the term *haustellum* refer to any ensheathed stylate mouthpart type, thus necessitating the term *haustorium* as a name for the proboscis of adult trichopterans and closely convergent mouthparts from a few other clades; (iv) that the term *glossate* be applied only to the characteristic, glossa-bearing mouthparts of certain adult aculeate hymenopterans; and (v) that the term siphonate refer to any galeal or labial structure that forms a tubular structure for fluid uptake. (See Table 7 for additional details.)

TABLE 7

STANDARDIZED NAMES USED FOR PROJECTING, FOOD-REACHING ORGANS DESCRIBED IN THIS STUDY

no.	*mouthpart class*	*common members*	*name for projecting, food-reaching organ**
8.	**Rostrate**	scorpionflies; lacewings	**rostrum**
9.	**Rhynchophorate**	weevils	**snout**
17.	**Haustoriate**	caddisflies	**haustorium** (not "haustellum" of other authors)
18.	**Labellate**	cyclorrhaphan flies, some nematoceran and brachyceran flies	**labellum**
19.	**Siphonate**	moths, skippers, butterflies	**siphon**
20.	**Siphonomandibulate**	blister beetles, wedge-shaped beetles	**siphon**
21.	**Glossate**	bees, vespid wasps, spoon-wing lacewings	**glossa**, tongue
24.	**Segmented Beak**	cicadas, hoppers, psyllids, aphids, whiteflies, bugs	**beak**
25.	**Buccal Cone**	sucking lice, elephant louse	**buccal cone**, labral cone
26.	**Mouthcone**	thrips	**mouthcone**
27.	**Monostylate/ Distylate**	robber flies, dance flies, bee flies	**proboscis**
28.	**Distylate/ Tetrastylate**	wood gnats, snipe flies, mydas flies, stiletto flies	**proboscis**
29.	**Hexastylate**	mosquitoes, moth flies, biting midges, horse flies	**proboscis**, fasicle, syntrophium
30.	**Tristylate**	fleas	**proboscis**
31.	**Tubulostylate**	tse-tse flies, louse flies, bat flies, sheep keds	**proboscis**
32.	**Siphonostylate**	noctuid moths	**siphon**

*Boldfaced designations are preferred and used in this study.

8.2. Nomenclature and Documentation of the Derived Groups

In the classification of insect mouthparts that follows, I have established and named two hierarchical levels. They are the more inclusive, or primary groups termed **series** and the more restrictive, or secondary, groups termed **classes**. The term "series" was established by Metcalf (1929) for two major mouthpart groups--hausellates and mandibulates, although it was abandoned in subsequent treatments (see Metcalf et al. 1962, James and Harwood 1969). For Metcalf, a series encompassed groups of mouthpart types that share a fundamental structural organization. Similarly, I am using the term class as a collection of mouthpart types that share a less fundamental feature or features and have membership in a particular series.

In this study a series is conceived as a basic head/mouthpart body-plan, characterized by structural similarities at the grossest of scales. Thus a series represents from one to 13 mouthpart classes that are sufficiently similar that the series, in effect, is characterized *a posteriori* by a unifying *gross* mouthpart morphology (see usage by Metcalf 1929). I have established mouthpart series to make general structural sense of the diverse assemblage of mouthpart classes and thus have grouped the 34 mouthpart classes into eight mouthpart series. Mouthpart series are generally revealed in the overall mouthpart class dendrogram of Fig. 28, but the correspondences to mouthpart classes are not exact for all series since series were independently established to accomodate mouthpart classes based on the presence of common structural themes.

The term "class" is operative at a lower level of morphological analysis and refers to major variations of mouthpart structure within the data-set. Differences among mouthpart classes within a series reflect significant modifications of the already established, major mouthpart structures, rather than radical change of the major mouthpart structures themselves. (Thus, mandible-bearing, filter-feeding dipteran larvae and silk-spinning panorpoid larvae both belong to a mandibulate series but are clearly differentiated from various stylet-bearing classes of another mouthpart series, such as the stylate-haustellate series, which bears dramatically rearranged mouthpart elements for piercing tissue. Table 5 presents a synopsis of the mouthpart series and classes resulting from this study.

I have applied those names to mouthpart classes that best describe or characterize an important or otherwise prominent structure or group of structures present in all members of that class. In some instances preference was given to terms previously used in the literature that refer to particular mouthpart types--e.g. "mortar-and-pestle" and "glossate." In other instances new terms were chosen to designate mouthpart types that either had a terminologically unacceptable prior name (hence substitution of "haustorium" for "haustellum" in forms with sponging hypopharynges), or had no previous designation (e.g. "sericterate," "siphonomandibulate," and "tubulostylate").

Geochronologic age information for fossil forms were based on the currently most acceptable stage-level interval encompassing the fossil forms. I am using a number, boldfaced in brackets, to refer to the specific insect deposits to which reference is made. These numbers refer to the Fossil-Insect Locality Register provided as Appendix E. Associated with discussions of the geochronology of mouthpart classes are cladograms depicting corroborated current hypotheses for the relationships of taxa within a mouthpart class. Superimposed on these cladograms are fossil occurrences of those lineages with fossil records. These occurrences are from the localities provided in Appendix E and the taxa and taxa reference sources for each occurrence is provided in Appendix F. Absolute ages are from Harland et al. (1982).

I have included for each mouthpart-class an overview (e.g. Fig. 29) detailing (i) a lateral profile drawing of a representative taxon illustrating the mouthpart class, (ii) a general taxonomic list of the members of the mouthpart class, (iii) geochronologic range of the mouthpart class, and a pie-charts detailing the distribution of (iv) functional feeding groups and (v) diets of members of the mouthpart class. Drawings accompanying the mouthpart class descriptions illustrate the general form and some important character-states of mouthparts and heads mentioned in the text. These illustrations are meant to depict species typical of their respective mouthpart class. The drawings are from taxa described from the data-set in Appendix B and are provided with data-entry numbers corresponding to Appendices B and C. Data from which functional-feeding-group and dietary data are derived from Appendix B, under the heading, "Dietary Data." Lastly, I have provided a dendrogram exhibiting the clustering relationships among members for each mouthpart class. The relationships of these dendrograms of mouthpart classes to each other is provided in a master dendrogram is given in Fig. 28.

8.3. Mandibulate Series

8.3.1. General Features of the Mandibulate Series

General Structure. Mouthparts of the Mandibulate Series are distinguished by presence of three pairs of gnathal segments: mandibles, maxilla and a labium. Mandibles and maxillae work as nonstyliform, paired elements or groups of elements that purchase, manipulate and comminute food. Mandibular and maxillary movement is overwhelmingly dominated by adduction and abduction; limited "protraction" can occur in entognathates. An unpaired labium serves as a lower "lip" that is complemented by the similarly unpaired labrum, or upper "lip" to assist packing and transportation of food orally. The suction mechanism for food ingestion is a pharyngeal pump, rarely a clypeal pump. The epipharynx and hypopharynx is usually well-developed, serving as a gustatory organ with mechano- and chemosensilla; however, other roles, such as filtering or silk-production, occur in a few classes. Other sensory functions are provided by paired and unpaired gnathal processes and appendages. Ancillary cephalic sensory structures include almost always a well-developed compound eye or larval stemmata, often ocelli and variously developed, generalized antennae receptive to diverse sensory imputs.

The key feature of the Mandibulate Series is presence of an adducting and abducting mandible involved in food acquisition dominantly by biting (the commonest mode) or some alteration thereof. In rhynchophorates this key feature is modified into boring, accompanied by rotation of the transverse adduction/abduction plane 90 degrees from the sagittal axis. In Pectinate, Mouthbrush and Mandibulobrustiate forms, setal combs replace mandibular teeth as the principal site of securing food. Modifications allowing for these and other varied modes of food acquisition are structural changes in mandible shape, dentition and vestiture, which are complemented by similar changes in other mouthparts, particularly the maxilla and labium. Structural co-optation of elements between or among mouthpart regions is absent; however, functional co-ordination of movement of elements within or among regions is highly developed.

Included Classes. Subdivisions of the Mandibulate Series are the Entognathate, Monocondylate, Adult Ectognathate, Larval Ectognathate, Maxillolabiate, Raptorial Ectognathate, Mortar-and-Pestle, Rostrate, Rhynchophorate, Pectinate, Mouthbrush, Mandibulobrustiate and Sericterate Classes. (See Table 5 for taxal membership, life-stages and number of taxa examined for each mouthpart class.)

Diversity and Other Distributional Patterns. The Mandibulate Series represents the greatest number of mouthpart classes (the Stylate-Haustellate Series contains nine classes, compared to the 13 of the Mandibulate Series). Since this series comprises virtually all orthopteroid forms, most larval and adult coleopterans and many of the remaining holometabolous larvae, it is the most abundant and diverse series in terms of species. Notably, most of these taxa reside in the Adult Ectognathate Class. All taxonomic orders, except advanced hemipteroids (thysanopterans, anoplurans, homopterans and heteropterans) are represented as a immature, adult, or both. This mouthpart series is the only one that is dominated by solid-food consumption; less commonly particulate matter is taken, especially in aquatic classes. Notably, four, or 30%, of the mouthpart classes in this series, are obligately associated with immature forms occurring in fully aquatic habitats.

Although typically associated with biting-and-chewing forms, many entognathates, adult-ectognathates and rhynchophorates, particularly cucujoid beetles, have important roles in the pollination of flowering plants. These members are floricolous species pollinating flowers of the cantharophilous pollination syndrome (Faegri and van der Pijl 1980). Cantharophilous flowers are characterized by large, bowl-shaped corollas with few visual attractants and by easily accessible pollen, nectar and sexual organs. These mandibulate, predominately "mess-and-soil" pollinators (Faegri and van der Pijl 1980) accomplish their task by consuming portions of the sexual organs and external floral appendages in return for transportation of pollen to conspecific flowers. This is in distinct contrast to members of the labellate, siphonate and glossate classes, wherein nectar or pollen is consumed with minimal damage to floral structure.

Major Structural Variations. There are four major modifications of stereotyped biting-and-chewing mouthparts within the Mandibulate Series. First, in rostrates, hypognathous prolongation of the head into a beak with basally-originating mouthparts, in conjunction with a powerful clypeal pump, has resulted in the ability to feed on fluidized tissue, especially carrion. Second, in rhynchophorates, there is prognathous prolongation of the head capsule into a snout that bears terminal mouthparts for boring indurated tissue. Thirdly, pectinate, mouthbrush and mandibulobrustiate forms have deployed mouthpart-associated tracts of spines, setae, hairs and bristles into particle-capturing organs. Movements of these mouthparts are co-ordinated to induce incurrent and excurrent water flow for efficient capture of particulate food. Lastly the Sericterate Class has modified the the labium and hypopharynx into a spinneret while maintaining the generalized mouthparts of holometabolous larvae as an efficient system for chewing externally and internally vascular plant organs. The remaining mouthpart classes are less modified than the three generalized classes--the Entognathate, Monocondylate and Adult-Ectognathate Classes--and involve less dramatic head and mouthpart restructuring.

Geochronologic Range. The solid-food-associated Mandibulate Series is the structural progenitor of other mouthpart series. These structurally derived mouthpart series are predominately liquid-feeders or, less commonly, small-particle feeders. The earliest known apterygote insects are of Early and Middle Devonian age (Shear et al. 1984, Labandeira et al. 1988) and were members of the Entognathate Class. The first appearance of pterygotes during the Namurian Stage of the Lower Pennsylvanian (Carpenter and Burnham 1985) already displayed well-developed mandibulate mouthparts assignable to the Adult Ectognathate Class. The Mandibulate Series has been dominant at least since the Middle Permian, during the radiation of several generalized, biting-and-chewing holometabolous orders (Smart 1963; Hennig 1981) and later diversified during the Mesozoic radiation of coleopterans (Crowson 1981).

8.3.2. Entognathate Class
(Class 1)

Description. Head spheroidal, nonprotractile; proboscis absent. Genae well-developed or absent; gula well- to minimally-developed. Antennae filiform or less commonly moniliform or papillate; ocellar structures numerous or absent; compound eyes moderately developed and dichoptic, or absent. Mouthparts mandibulate, entognathous, mostly forwardly-directed, symmetrical and nonretractile; food pump clypeo-labral or not evident.

Clypeus generally transversely elongate and undivided, rarely otherwise. Labrum quadrate, undivided, and margin straight to shallowly curvilinear. Hypopharynx lingulate or less often bilobed with superlingulae; epipharynx generally membranous. Mandibles monocondylic; incisiform with or without a molar region; musculation of abduction/adduction. Maxillae with main-body of two sclerites; stipes elongate to rodlike; bearing galea, lacinia and palp, or apalpate and bearing laciniae and galeae only or laciniae only. Maxillary palp, when present, generally papillate or mucronate, 1- to 3-segmented; mostly short in length. Galeae a generalized lobe; laciniae variously modified. Labrum with elongate or equant, subdivided main-body; bearing glossae or a ligula, rarely with palps. Labial palp 1-segmented, papillate and short, or more commonly absent. Glossae setate or generalized; paraglossae absent, or when rarely present, generalized. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. Several unique structural developments are jointly restricted to entognathates. These key phenocharacters include

(i) a ventral cephalic sac housing externally inconspicuous mouthparts, (ii) a unique hypopharyngeal and maxillary mechanism that is protracted and retracted by elongate and articulatory rods and (iii) small body size. Mandibular monocondyly is associated with entognathates, but also occurs in monocondylates and stylate-entognathates. Although some of these features, particularly entognathy and mandibular monocondyly, appear in a few pterygote groups, they are nevertheless acquisitions for very different mouthpart structures and feeding mechanisms.

Diversity and Natural History. Entognathates are collembolans (neanurids excluded) and diplurans. They play a salient role in the microarthropod fauna inhabiting litter, soil and wood by breaking down plant material and feeding on fungi. Their diet consists of varied plant, animal and fungal detritus (Fig. 29). Both immatures and adults comprise this group. When compared to other mouthpart classes, entognathates are taxonomically minor, comprising an estimated 0.8% of extant species (Table 5, Fig. 131). Although unimportant in terms of taxonomic diversity, some species of collembolans are some of the most abundant hexapods known and can occur in extremely high densities in the litter and upper topsoil fauna (Little 1983). They constitute a major portion of the biomass responsible for degradation of litter into humus in various nonarid environments (Little 1983) and probably are the principal consumers of edaphic fungi in some mesic regions (Moore 1988).

Structural Themes. Three major themes are evident within entognathate mouthparts, as indicated by the subclustering patterns in Fig. 30. An analysis of the variables in the data-set reveals that 16

CLASS 1: ENTOGNATHATE

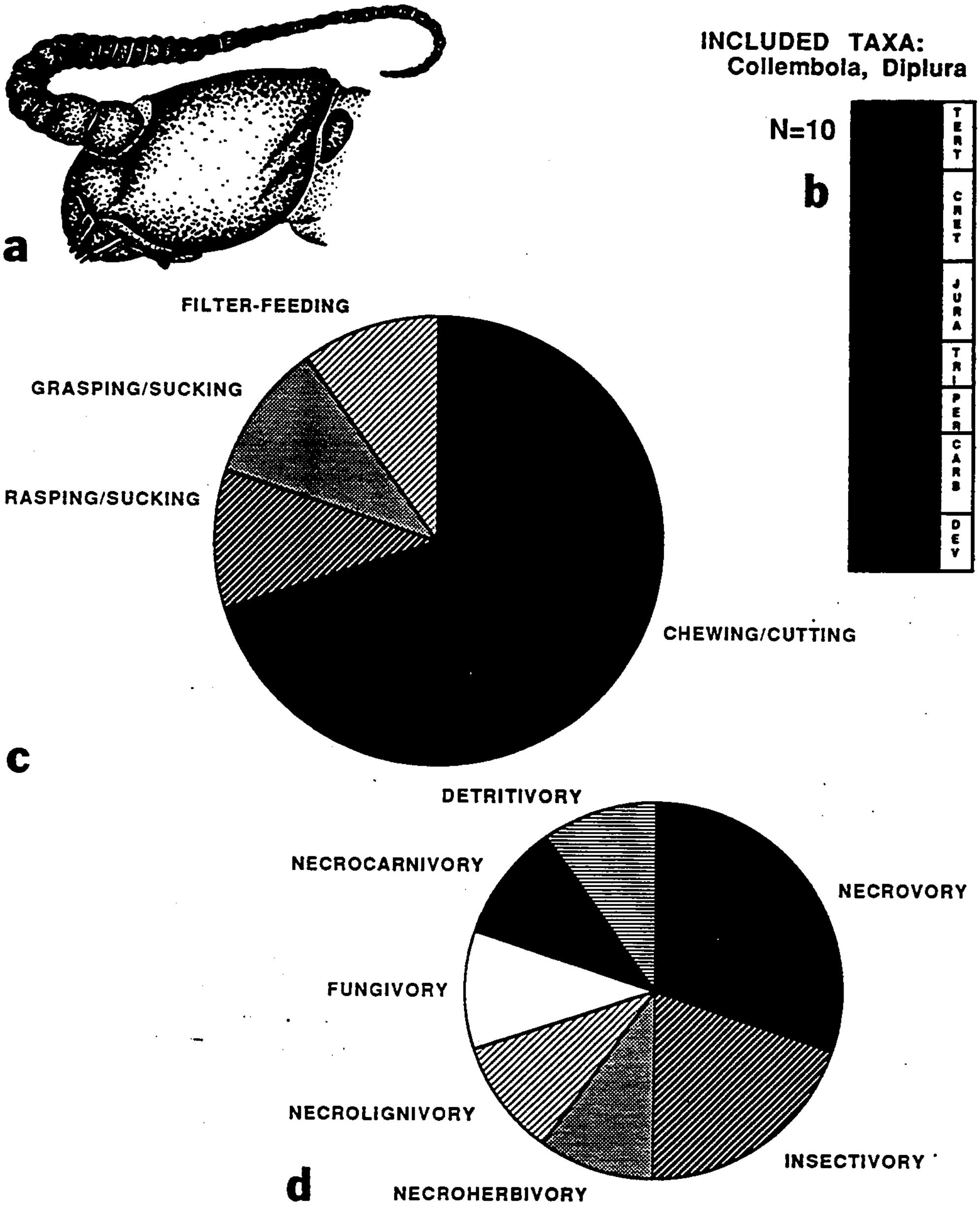


FIGURE 29. Overview of the Entognathate Mouthpart Class. a, *Campodea chardardi* Condé (Diplura: Campodeidae, data-set no. 12), after Francois (1970); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

characters contribute disproportionately to subcluster formation. These characters are distributed over all nine mouthpart regions, but overwhelmingly emphasize mandibular and labial differences.

In Fig. 30 the three subclusters can be viewed from left to right. Subcluster 1 consists of six collembolan species (bracketed by data-set nos. 4 to 11 in Fig. 30). This subcluster consists of hypogasturoid, entomobryoid, anurid neoarthropleonan and sympleonan collembolans exhibiting entognathate mouthparts specialized for chewing. Subcluster 2 consists of three dipluran taxa (data-set nos. 12 to 14) that are characterized by the absence of eyes and presence of labial palps, unlike Subcluster 1. Subcluster 3 is a specialized anurid collembolan, *Brachystomella parvula* (taxon 8), that lacks mandibles and maxillary palps, unlike Subclusters 1 and 2. Apparently mouthpart structure in the Anuridae is quite plastic since another confamilial is a piercer-and-sucker and a member of the Entognathous-Stylate mouthpart class (Section 8.8.2).

Geochronologic History. Entognathates have one of the earliest documented occurrences in the fossil record of any mouthpart class (Fig. 31). On comparative morphological, embryological and paleontological grounds, there is no reason to believe that they are preceded in the fossil record by any of the other 34 mouthpart classes, except possibly for the entognathous-stylates (see Section 8.8.2). Their earliest occurrence is a mouthpart-bearing collembolan *Rhyniella praecursor* Hirst and Maulik 1926 from the Lower Devonian Rhynie Chert of Scotland [104] (Hirst and Maulik 1926, Whalley and Jarzembowski 1981, Greenslade 1988)

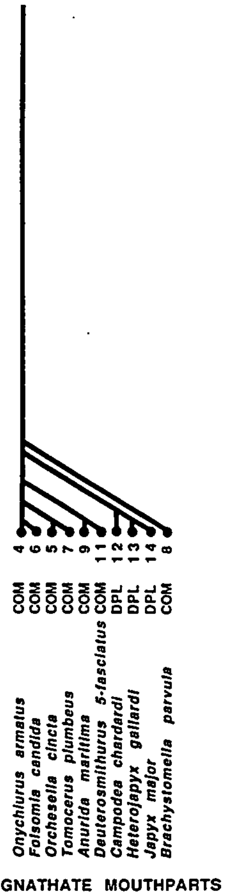


FIGURE 30. Cluster analysis dendrogram of taxa comprising the entognathate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

(Fig. 31). A relatively large entognathate is known from the Carboniferous of Illinois [96] (Kukalová-Peck 1987) the earliest known dipluran. Other notable fossil entognathates include the earliest occurrence of an arthropleonan collembolan, an entomobryid from the Lower Permian of South Africa (Riek 1976) and the earliest known symphypleonan collembolans, consisting of about a dozen species found in Baltic amber [19] (Handschin 1926a, 1926b, 1926c; Crowson et al. 1967; Larsson 1978).

Previous Designations. Entognathous mouthparts are a relatively recent concept. They were first seriously discussed as a unique mouthpart type as the "entognathy" of Manton (1964, 1977, 1979) and the *entognathie* of Denis and Bitsch (1973). They were not mentioned by Metcalf (1929), Metcalf et al. (1962), or Smith (1985); however, Snodgrass (1952) and Matsuda (1965) provided cursory discussions of entognathy. Traditionally, in major text-books entognathates have been considered as a subtype of "mandibulate" mouthparts, usually without any discussion of the special features of entognathate stylets (e.g. James and Harwood 1969, Borror et al. 1976, Ross et al. 1982). (See Table 6 for details.)

Because collembolans and diplurans of this mouthpart class represent the stereotypical entognathate condition, I am using the term **entognathate** as a designation for the mouthpart class discussed in this section.

Review of Literature. Literature on the mouthpart structure and diet of the Entognathate Class is scant and most of it is old. Folsom (1899, 1900), Hoffman (1905, 1908, 1911), Bitsch (1928) and Silvestri

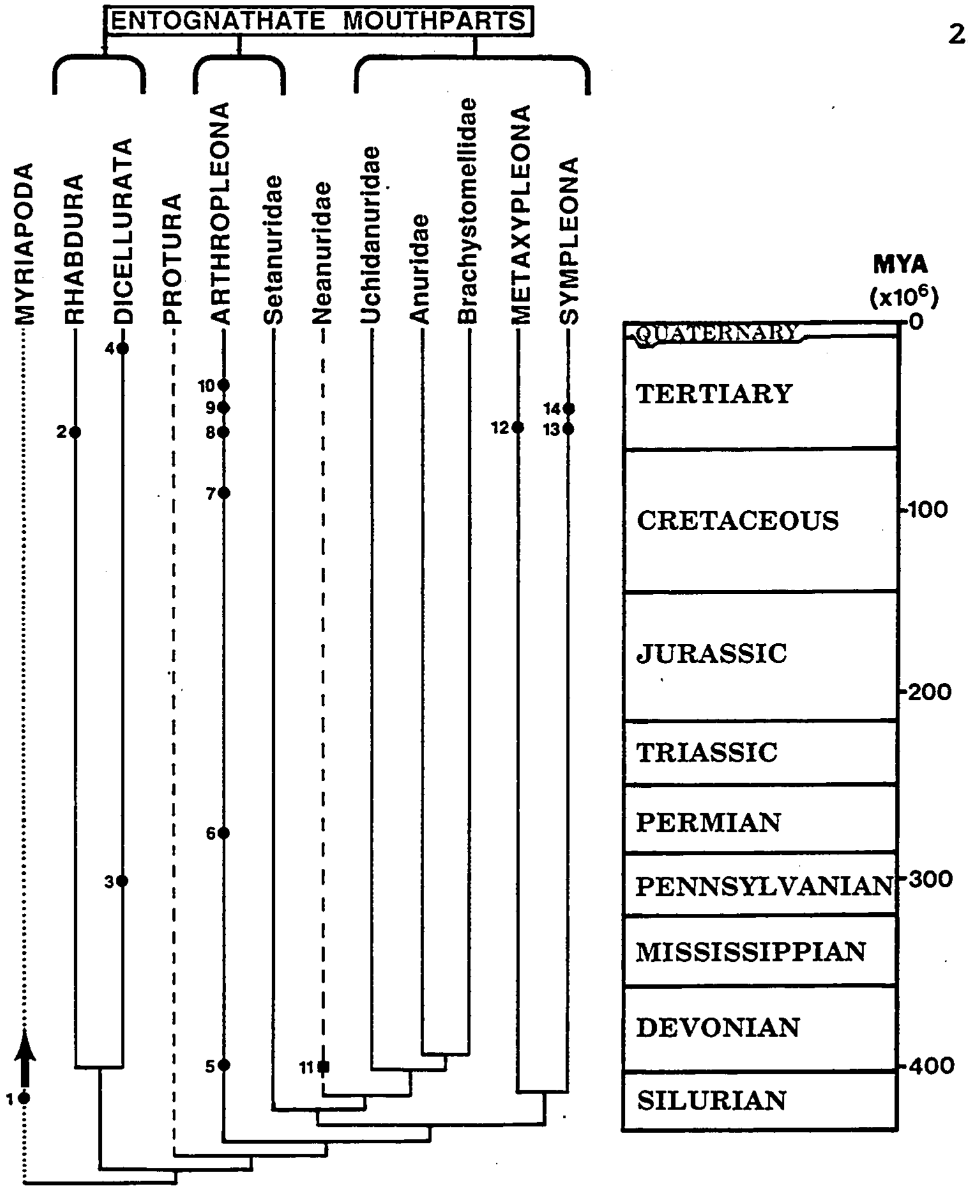


FIGURE 31. Geochronologic history of the Entognathate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Schaller (1970), Kristensen (1981), Kukalovà-Peck 1987 and Labandeira, Beall and Huber, in prep. The taxonomic level of analysis is the suborder and family. The outgroup is Myriapoda. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

(1933) were the first major researchers to describe entognathate mouthpart structure systematically in monographic form. Later, Jeannenot (1956), Schuller and Wolter (1963), Manton (1964, 1977, 1979) and Goto (1972), among others, described the mouthpart structure of certain entognathate species, often emphasizing function as a way of making sense of complex mouthpart structure.

8.3.3. Monocondylate Class
(Class 2)

Description. Head quadrate, with a short proboscis and anterior prothoracic margin enveloping the dorsal head region. Genae moderately- to well-developed; gula absent. Antennae setaceous; ocelli 3 or absent; compound eyes expansive and holoptic. Mouthparts hypognathous, mandibulate, symmetrical and nonretractile.

Clypeus quadrate, single. Labium quadrate, single; margin straight to curvilinear. Hypopharynx trilobed; epipharynx generally forming ventral part of food pump, bearing a prelabral gutter. Mandibles monocondylic; molariform or incisiform; musculation of adduction/abduction. Maxillae with galeae, laciniae and palpi. Maxillary palpus long, mucronate, with more than 6 segments. Galeae generalized and lobate; laciniae generally bearing spinose processes or setae. Labium vertically elongated, with 3 basal segments and a full complement of glossae, paraglossae and palps. Labial palps clavate to mucronate, intermediate in length and composed of 4 or more segments. Glossae subdivided into two generalized lobes; paraglossae spatulate. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. Monocondylate mouthparts and head structure is unique within hexapods (Fig. 33) and is characterized by a combination of ectognathous mouthpart placement and mandibular monocondyly. In addition, the mandibles are elongate but not stylate and the hypopharynx is trilobed. The labial and maxillary palps have supernumerary segments when compared to other mandibulate mouthpart classes and the maxillary palps are leglike. Each glossa is uniquely divided into two general lobes. Lastly the dorsal cranial region is covered by a shield-like extension of the anterior prothorax.

Monocondylates can only be confused with entognathates (Section 8.3.2) or adult-ectognathates (Section 8.3.4). Monocondylates differ from entognathates by possession of ectognathous rather than entognathous mouthparts, a long, leglike maxillary palp and subdivided glossae. Monocondylates are differentiated from adult-ectognathates by the presence of monocondylous instead of dicondylous mandibles, supernumerary maxillary and labial palp segmentation and a consistently trilobed hypopharynx. Additionally there are major differences in the construction of the cephalic endoskeleton (tentorium) among the three groups (Lauterbach 1972).

Diversity and Natural History. Members of the Monocondylate Mouthpart Class are diminutive, inconspicuous inhabitants of ground surface litter, interstices in upper soil strata and rocky areas of several aquatic habitats. These habitats notably include the rocky supralittoral zone surrounding most oceans of the world (Delaney 1954, 1959, 1960), scree areas of temperate mountains and highlands

(Janetschek 1954, 1955) and innundation- and dryland-forests of the Amazon Basin (Sturm 1984, Adis and Sturm 1987). Undoubtedly further studies of monocondylates in other regions of the world will document a broader ecological distribution. Monocondylates consist entirely of members of the Order Archaeognatha (bristletails), which translates to a diversity of two families, 50 genera and 414 described species (Appendix D) and a rank-ordering of 33 out of 34 mouthpart classes (Table 5, Fig. 131). Of the two families, the Meinertellidae are centered in the Indo-Malayan and Australian regions, with a strong secondary center in South America (Sturm 1984, Kaplan 1985) and the more temperate occurring Machilidae are centered in the Holarctic Region (Kaplan 1985). Apparently several species are parthenogenic (Wygodzinsky and Schmidt 1980).

Although generally considered detritivores (Wygodzinsky 1944), monocondylates consume a wide spectrum of live and dead foods as a group (Fig. 32). According to Willem (1924), *Petrobius maritimus* (Leach) consumes algal fragments of *Fucus*, *Ulva*, *Laminaria*, assorted chlorophytes and *Pleurococcus*. Delany (1954) found the conjugate alga *Zygogonium*, the byrophyte *Sphagnum* and various unidentified angiosperm remains in the gut of *Dilta littoralis* (Womersley). For *Petrobius brevistylis* Carpenter and *P. maritimus* Delany (1959) assigned their diets to scavenging and herbivory, to which Little (1983) added unicellular algae, lichens and mosses (cf. Willem [1924] above). Wygodzinsky (1944) summarized the diet of Brazilian machilids as consisting of dominately cryptogams (fungi, algae and lichens), fragments of phanerogams, *Pleurococcus* and significant mineral matter. Although Eisenbeis and Wichard (1987) state that machilids feed on algae and lichens, it is

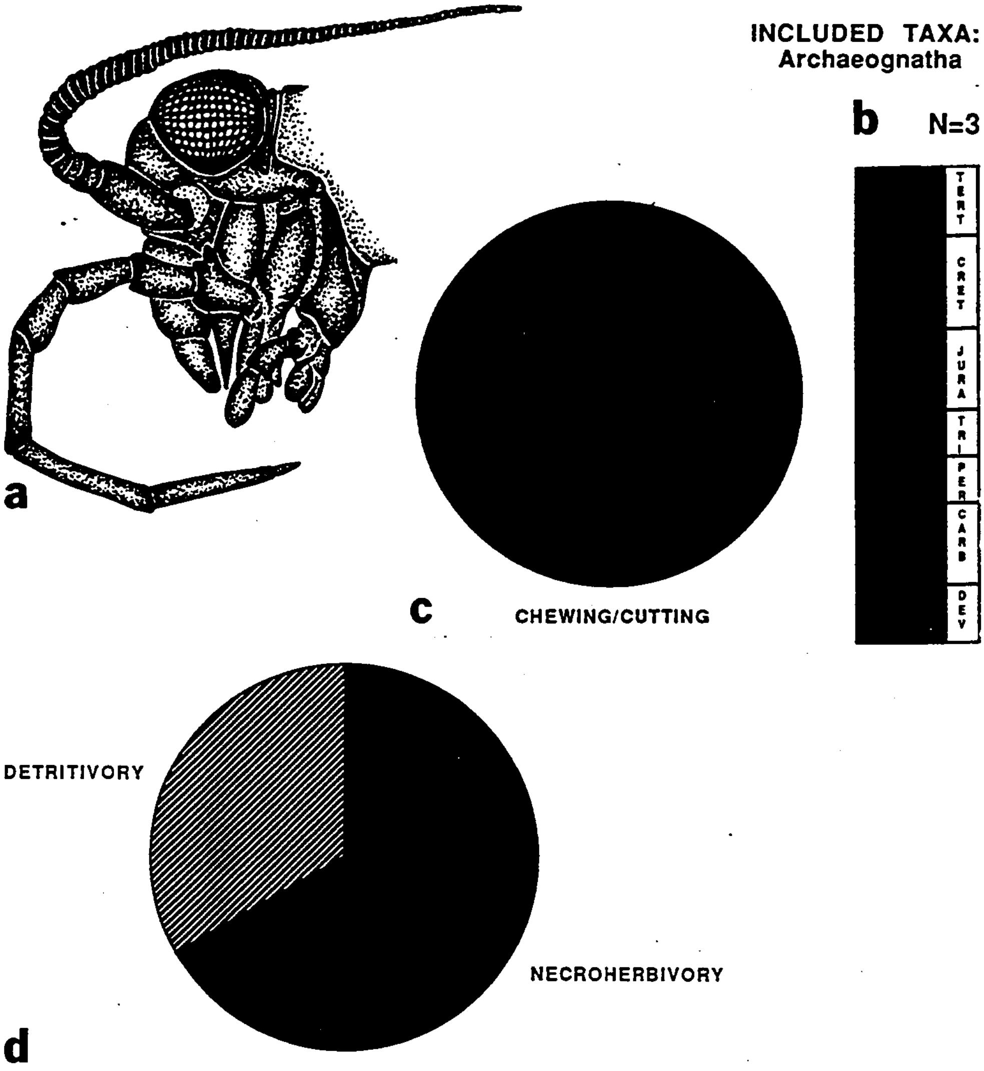


FIGURE 32. Overview of the Monocondylate Mouthpart Class. a, *Machilis* sp. (Archaeognatha: Machilidae, data-set no. 15), after Snodgrass (1928) and Bitsch (1956); b, taxonomic distribution, number of taxa examined and geochronologic range; c: functional-feeding-group; d: dietary spectrum.

clear that as a group the diet of monocondylates is best characterized as detritivorous, opportunistic and eclectic for most species. This general detritivorous feeding guild is exemplified by the mouthpart structure of monocondylates, which are characterized by weak, milling mandibles incapable of powerful abduction, and palpiform, often subsegmented, fleshy exites and endites of the maxilla and labium. These structures are designed to handle soft and digestible food that requires minimal preparation prior to consumption. Machilids are heavily preyed upon by arachnids (Wygodzinsky 1944, Delany 1959).

Environments preferred by monocondylates have high humidities, such as 30 to 60% for four machilid species studied by Sturm (1955) and, 70 to 85% for archaeognathans in general (Little 1983). Apparently archaeognathans do not drink water but can regulate water balance by uptake from paired, eversible abdominal vesicles (Smith 1970, Little 1983). Archaeognathans are nocturnal and are well-sighted since they have the most well-developed, massive compound eyes of any known flightless hexapod. While a peculiar sense organ on the second segment of the maxillary palp is of unknown function (Evans 1928), a distinctive papillate sensory complex on the labial palp is interpreted as a contact chemoreceptor (Eisenbeis and Wichard 1987). The often noted habit of "jumping" by archaeognathans is accomplished by extension of the ninth abdominal styli (Eisenbeis and Wichard 1987); these styli have also been interpreted as supportive skids on which the abdomen rests (Smith 1970).

Structural Themes. No structural themes are evident within the structurally well-integrated Monocondylate Mouthpart Class (Fig. 33).

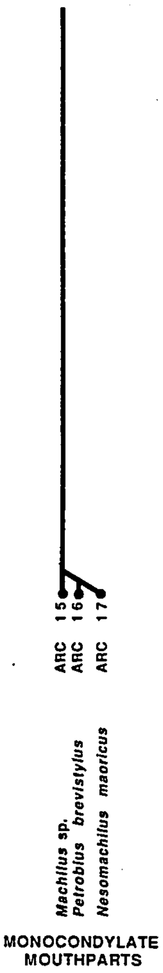


FIGURE 33. Cluster analysis dendrogram of taxa comprising the Monocondylate Mouthapart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

Geochronologic History. Monocondylates are geochronologically the oldest mouthpart class of insects and probably originated during the Late Silurian sometime before their first occurrence as fossils from the Early Devonian of Québec [**103**] (Labandeira et al. 1988, Shear 1990). Phylogenetic and other types of analyses reveal that the monocondylate head and mouthpart condition is plesiomorphic for insects (Boettger 1958, Kristensen 1981, Boudreaux 1987, Labandeira et al., submitted). Some of these features previously have been cited as plesiomorphic, including compound eyes (Paulus 1974), the pleural duplicature of the cranium (Lauterbach 1972) and a leglike maxillary palp (Kukalová-Peck 1987). Entognathate and entognathous-stylate mouthparts (Sections 8.3.2 and 8.8.2) occur in the sister-group to the insects, the Parainsecta, and first appear in a deposit slightly older than the first occurrence of monocondylate mouthparts, the Rhynie Chert [**104**] of Early Devonian age (Whalley and Jarzembowski 1981, Greenslade and Whalley 1986, Greenslade 1988, but see Crowson 1985).

The earliest monocondylate is *Palaeoectognatha gaspea* Labandeira, Beall and Hueber 1988, from the Lower Devonian of Québec [**103**], which is accomodated by a monotypic family (Fig. 34). Although machilid monocondylates appear as scraps of cuticle from the Middle Devonian of New York [**102**] (Shear et al. 1984), they do not first appear as substantive fossils until the Late Carboniferous of Illinois [**96**] (Kukalová-Peck, pers. comm.) and are followed by a long hiatus, reappearing in much younger amber deposits. (The record of a presumptive machilid from the Triassic of the USSR [Sharov 1948, Palct 1972) is erroneous and is now

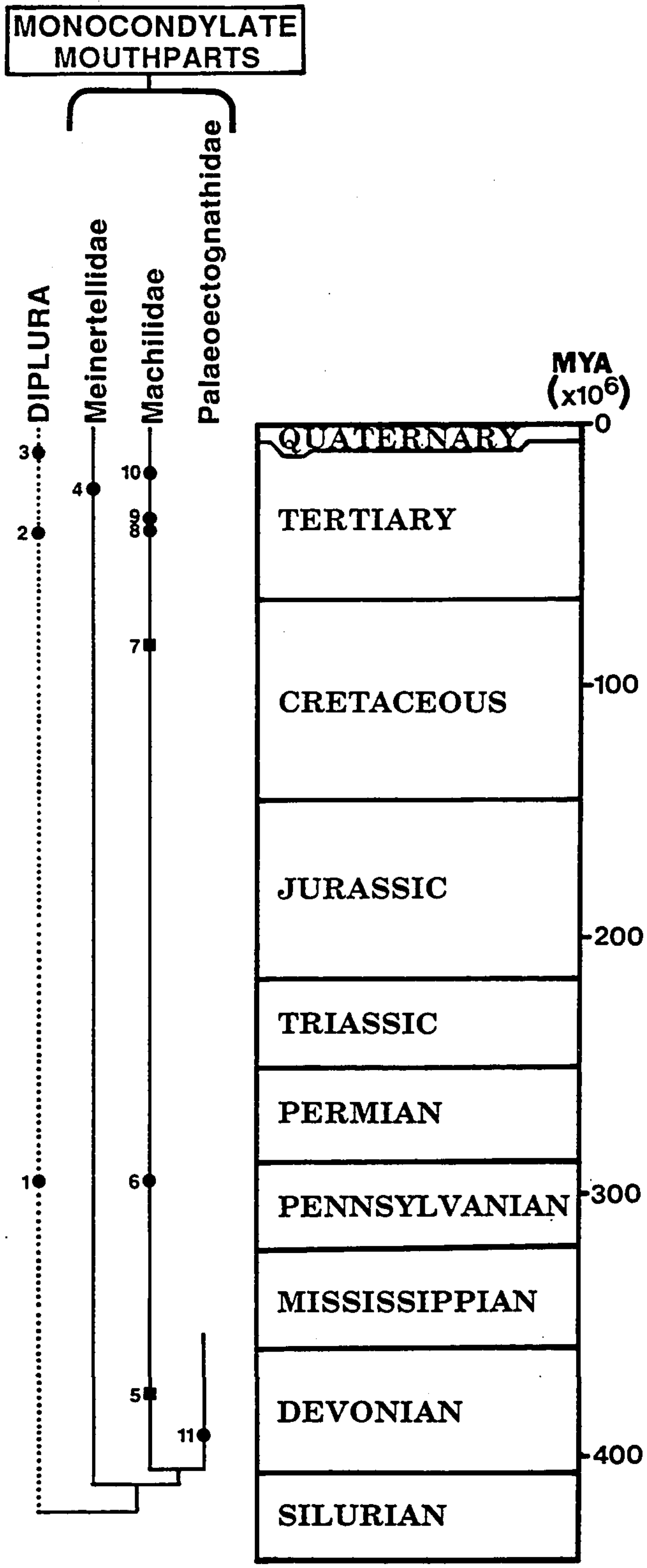


FIGURE 34. Geochronologic history of the Monocondylate Mouthpart Class. See Appendix F for taxa, localities, and references corresponding to each fossil occurrence. The phylogram is after Labandeira et al. in prep. The taxonomic level of analysis is the family; outgroup is Diplura. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.

considered to be an ephemeropteran naiad [Kukalová-Peck 1988, in litt.].) Machilids probably occur in Upper Cretaceous Siberian amber [37] (Zherikin and Sukacheva 1973) and are convincingly documented from the mid-Tertiary, with modern genera present in Upper Eocene/Lower Oligocene Baltic amber [19] (Olfers 1907), and unassigned genera occurring in Upper Eocene to Lower Miocene Dominican amber [17] (Schlee and Glockner 1978) and Lower Miocene amber deposits from Germany [6] (Schumann and Wendt 1989). Meinertellids occur in Upper Oligocene to Lower Miocene Mexican amber [11] (Wygodzinsky 1971). In general the fossil record of monocondylates is poor.

Previous Designations. The term monocondylate refers to the characteristic single condylar articulation of the mandible to a socket on the pleurostoma of the cranial capsule. This term has been used in a structural sense, but has never been regarded as a descriptor of a mouthpart class. Nevertheless mandibular monocondyly distinguishes members of the herein designated group from all other hexapod mouthpart types. Although entognathates (Section 8.3.2) and entognathous-stylates (Section 8.8.2) have mandibular monocondyly, and several stylate-haustellate mouthpart classes have secondarily derived monocondyly (Section 8.9), these mouthpart classes possess other features to sufficiently differentiate them from monocondylates (see "Key Pheno-characters" of this section). Thus the term **monocondylate** appropriately describes members of this mouthpart class. (See Table 6 for a history of monocondylate nomenclature.)

Review of Literature. In spite of the depauperate taxonomic diversity and inconspicuous habits of monocondylates, there has been considerable study of their mouthpart structure, especially for machilids. Major contributions toward the study of monocondylate mouthparts have been made by Baer (1912), who interpreted anatomic sections of heads; Chaudonneret (1948, 1956), Bitsch (1956, 1960, 1963) and Wygodzinsky (1944, 1945, 1948) who described numerous species of machilids, illustrating their head and mouthpart structure; and Larink (1971) and Snodgrass (1928, 1935) who emphasized the phylogenetic importance of machilid head and mouthpart structure for insect evolution. Meinertellids have been investigated minimally, although Mendes (1981) recently has included head and mouthpart descriptions of meinertellids from Viet Nam. Excellent scanning electrom micrographs of machilid mouthparts may be found in Eisenbeis and Wichard (1987).

8.3.4. Adult-Ectognathate Class
(Class 3)

Description. Head spheroidal with rostrum short or absent; nonretractile; rarely with anterior prothoracic shield over dorsum. Genae prominent to minimally-developed, rarely absent; gular region prominent and well-developed. Antennae mostly filiform, setaceous, or moniliform, but also clavate, lamellate or serrate; ocelli frequently absent, less commonly 3; compound eyes moderately developed and dichoptic, rarely otherwise. Mouthparts mandibulate, prognathous or hypognathous, symmetrical and nonretractile. Food pump generally pharyngeal.

Clypeus transversely elongate; generally undivided but occasionally subdivided or fused to frons. Labrum quadrate or vertically elongate; undivided; bearing a pectinate or straight to curvilinear margin. Pharyngeal region capacious; hypopharynx lingulate, often adjoined to labrum or labium, rarely bilobed or a membranous surface; epipharynx mostly membranous. Mandibles dicondylic; tetragonal or falcate; edentate or dominated by an incisor region, but also molariform, serrated, incisiform with a mesial brush, or caniniform; musculated for adduction/abduction. Maxillae with equant to elongate stipes; a main-body of 4, rarely 3 or 2, sclerites; bearing galeae, laciniae and palpi. Maxillary palpus filiform-moderately clavate, rarely mucronate or filiform-strongly clavate; 4- or 5-semented; intermediate to long in length. Galeae variable; laciniae often with mesially-directed spines or setae, infrequently fimbriate or absent. Labium with a main-body that is 2- or 3-divided, elongate to rarely equant or extremely elongate; bearing glossae, paraglossae and labial palps, with glossae and/or paraglossae uncommonly fused into a ligula. Labial palpus filiform, rarely mucronate or clavate; 3-segmented; intermediate to long in length. Glossae variable; paraglossae frequently absent, but when present generalized, lingulate or fused to glossae as a ligula. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. Adult-ectognathates are a diverse but unique component of the Mandibulate Series. They are the most generalized of the mandibulate mouthpart classes and are characterized by generally unfused mouthpart elements that are never structurally adjoined to mouthparts in adjacent regions, although they typically exhibit functional coordination. The maxillae and labium of adult ectognathates possess two mesial endites (infrequently fused into a mala) and a palpus, analogous to the structure of the primitive arthropodan limb. Furthermore the adult-ectognathate cranial capsule lacks the wide, flaring and conjoined genae that subtends a triangular frontoclypeal sclerite in larval ectognathates (Section 8.3.5). Instead adult-ectognathates possess a substantively different system of cranial sutures and sclerites. Since virtually all members are trophic in their adult stages, there is no reduction of mouthpart elements or regions, unlike taxa from mandibulate classes.

Other mandibulate mouthpart classes can be distinguished from adult-ectognathates by the absence in adult ectognathates of various specially modified mouthpart elements, or the absence of fusions between or among mouthpart regions. Since adult-ectognathates bear dicondylic mandibles, they can be differentiated from entognathates and monocondylates (Sections 8.3.2 and 8.3.3) which lack mandibular condyly. Adult-ectognathates also lack the specialized maxillary and labial elements of adult raptorial-ectognathates (e.g. unsegmented maxillary palp adjoined to the mala and the glossoparaglossae) and the unique labial mask of immature raptorial-ectognathates (Section 8.3.7). Additionally, adult-ectognathates lack pectinate or brustiate appendages that are used for filter-feeding in the pectinate and mouthbrush classes (Sections 8.3.11 and 8.3.12). These include labral fans and penicillate prosthecate mandibles. Also absent from ectognathates are proboscideal extensions of the head found in rostrates and rhynchophorates (Sections

8.3.9 and 8.3.10). In terms of fusions between or among mouthpart regions, adult-ectognathates lack the maxillolabial complex of maxillolabiates (Section 8.3.6), the unique epipharyngeal/hypopharyngeal ball-and-socket masticatory apparatus of the Mortar-and-Pestle class (Section 8.3.8), and the silk- spinning labiohypopharyngeal complex of mandibulobrustiates and sericterates (Sections 8.3.13 and 8.3.14).

Diversity and Natural History. Adult-ectognathates consist of insects belonging to virtually all major mandibulate groups, namely thysanurans, blattodeans, mantodeans, phasmatodeans, orthopterans, isopterans, dermapterans, embiopterans, adult and naiad plecopterans, zorapterans, larval and adult megalopterans and raphidiopterans, most adult planipennians, most adult coleopterans, adult zeuglopteran lepidopterans and adult symphytan and parasitican hymenopterans. Adult-ectognathates represent an estimated 21.3% of all data-set taxa (Table 5), which corresponds to approximately 24% of all species in the modern hexapod fauna (Fig. 131). These data indicate that adult-ectognathates are the most taxonomically diverse mouthpart type (Fig. 131). The high diversity of this mouthpart class is demonstrated by its abundance of taxa, including 17 orders, 331 families, 35,150 genera and approximately 363,500 species (Appendix D). Within this mouthpart class, adult coleopterans contribute disproportionately to this diversity. Adult-ectognathates constitute both immature and adult forms of nonholometabolous forms and only the adult members of holometabolous forms, with the sole exception of megalopteran and raphidiopteran larvae. These latter two exceptions bear close resemblances to their respective adult stages, unlike other holometabolous groups. As a group, adult-ectognathates are usually conspicuous, medium- to large-sized insects with broad dietary preferences for solid food.

The dietary breadth of adult-ectognathates involves virtually every major terrestrial and freshwater food resource and many incidental food resources (Fig. 35). Members of this mouthpart class have dominant roles in stable, long-term habitats, but are also plentiful in ephemeral and patchily-distributed microhabitats. Relatively stable, long-term (though often seasonal) habitats include feeding on pollen and nectar, consumption of various plant organs by external feeders and predation on live insects. Ephemeral microhabitats most notably are fungi, dung and carrion.

Pollinivory and anthophily in beetles is a much discussed topic, especially since previously attention has been focused on more apparently coevolved systems, such the faithful pollination of flowering plants by siphonates and glossates (Sections 8.6.2 and 8.7.2). Flower-frequenting coleopterans occur as two ecologically-differentiated groups: a taxonomically diverse group that visits flowers for adult feeding and a less diverse group whose larvae develop within flowers or fruits (Crowson 1981). Consumption of pollen by these forms however requires special modifications, including the cracking of pollen grains by the mandibles of small species, and the direct consumption of pollen by large species followed by intestinal germination and subsequent attack by intestinal enzymes (Crowson 1981). In this context Proctor and Yeo (1973) and Faegri and van der Pijl (1980) have established several features of pollinating coleopterans and coleopteran-pollinated

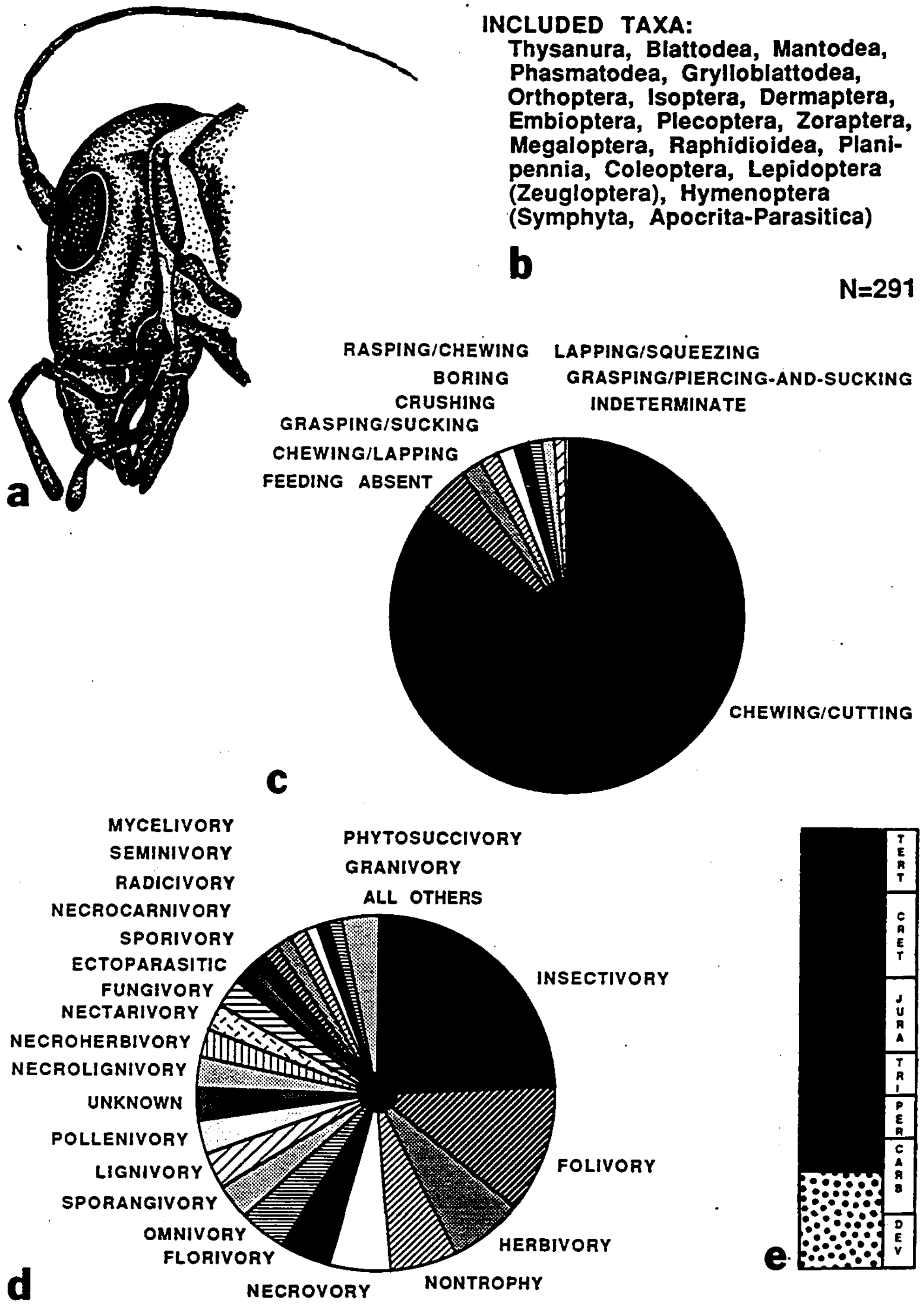


FIGURE 35. Overview of the Adult Ectognathate Mouthpart Class. a, *Ambylocorypha oblongifolia* (DeGeer) (Orthoptera: Phaneropteridae, data-set no. 103), after Kramer (1944); b, taxonomic distribution and numbers of taxa examined; c, functional-feeding-groups; d, dietary spectrum; e, geochronologic range.

flowers that define a "beetle pollination syndrome" or cantharophily. Floral features designed for beetle pollination include flowers grouped into capitate or otherwise bunched inflorescenses, floral coloration of white to rarely yellow, carpels that are either inferiorly located or raised above the stamens by a stout column, prolific production of pollen and de-emphasis of nectar production, and an open and radially symmetrical flower. Anthophilous coleopterans usually bear large, finely-facetted compound eyes; long, filiform or serrate antennae; elongate and hairy maxillary lobes and ligula; head tending toward a proboscate condition; well-developed powers of flight; and an elongate body shape. Both floral and pollinator features indicate that beetles lack color vision and visual acuity, prefer pollen over nectar consumption, must be protected from ovaries of seeds in carpels because of potential damage to the plant from slashing mandibles, and require an open, bowl-shaped flower for entry to the pollen-bearing organs. The role of cantharophily in flowering plant evolution is important (but see Grinfel'd 1975), particularly since many extant families of apomorphic polyphagans are dominated by pollinivorous taxa and several families are obligatly pollinivores (after Kevan and Baker 1983). Other adult-ectognathates have been observed as casual pollinators, including adult plecopterans, orthopterans, adult planipennians and raphidioipterans, micropterygid lepidopterans and symphytan hymenopterans (Porsch 1958, Grinfel'd 1959b).

The external plant-feeding insect guild is dominated by adult-ectognathates and sericterates (Section 8.3.14). Of the adult-ectognathate component, orthopterans, phasmatodeans and many families of polyphagan coleopterans constitute the major consumers of leafy and wood vegetation in most terrestrial plant communities (Bernays and Barbehenn 1987, Stork 1987, Tabashnik and Slansky 1987). Examples of the dominance of phytophagous adult-ectognathates in specific plant communities include the stem-boring guild in prairie annuals of Tall Grass Prairie in Illinois (Rathke 1976) and external foliage feeders on a *Baccharis* scrubland in southern Texas and northern Mexico (Palmer 1987).

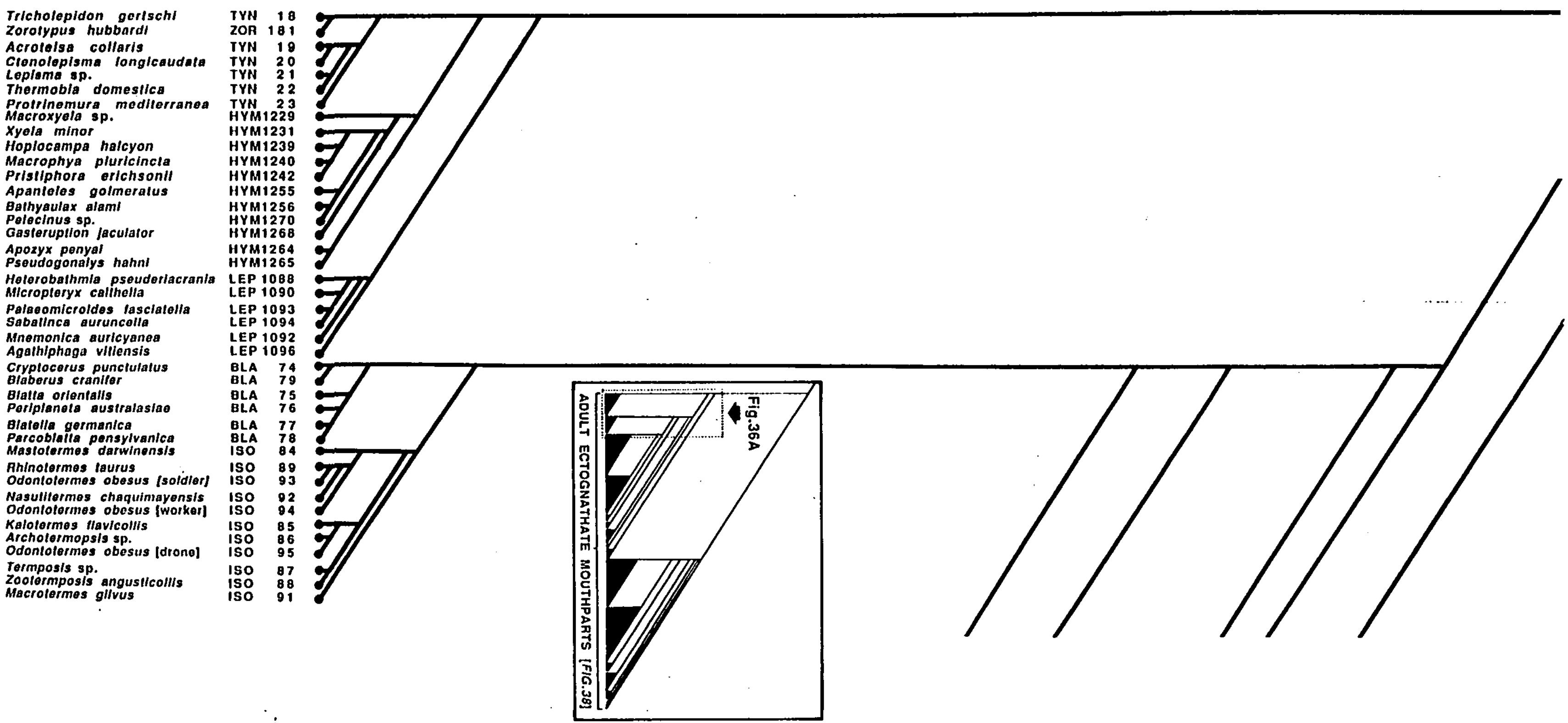
Adult-ectognathates that feed predominately on terrestrial and freshwater arthropods are a major food guild in many ecosystems. This guild includes tropical blattodeans, mantodeans, some dermapterans, raphidiopterans, the adults of planipennians, many adephagan and plesiomorphic polyphagan coleopterans, and some parasitican hymenopterans. (Clausen 1940, Braack 1987, Hagen 1987, Sih 1987, Stork 1987). Those adult-ectognathates that feed on other animals almost always feed on other insects and, to a much lesser extent, on noninsectan arthropods, snails and slugs and earthworms. Structural modifications for carnivory include a prognathous head; large, falcate, widely abducted mandibles; and long, agile palps. In general two behavioral strategies have evolved to secure prey: ambush predation whereby prey is secured by sudden surprise from a haunt, and pursuit predation wherein the victim is actively chased.

With regard to spatiotemporally confined habitats, fungi, dung and carrion are obvious candidates. Adult-ectognathate fungivores are mostly small archostemmatan and apomorphic polyphagan coleopterans which are intimately involved with the occupation, consumption and spore dispersal of ephemeral slime molds (Wheeler 1984), bread molds (Sinha

1968) and various mushroom and shelf fungi (Ashe 1984, Kukor and Martin 1987). Similarly, stercovorous beetles are prominent players in the mechanical disintergration of dung from grassland and savanna ruminant mammals (Halffter and Edmonds 1982, Hanski 1987). Another ephemeral habitat is the carrion community, wherein successive waves of insects invade carrion in various stages of decay (Payne 1965). In these microhabitats adult-ectognathates become dominant in the later successional stages and often undergo intra- and interspecific competition for limited food resources. After carcasses have become defluidized, many larval and adult coleopterans feed on dried tissue, skin, keratin and other substances (Smith 1986, Peschke et al. 1987, Braack 1987).

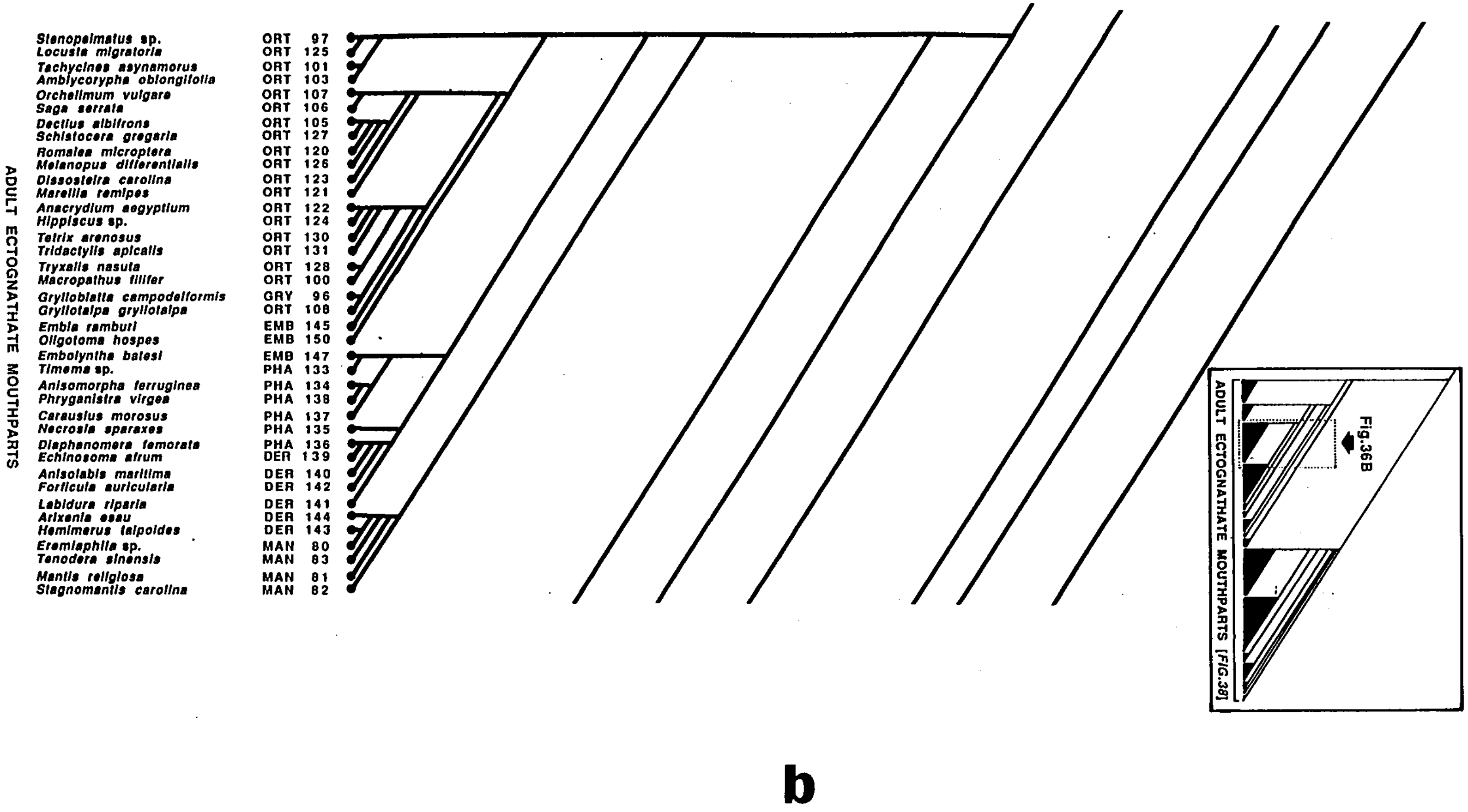
Structural Themes. Of the 34 mouthpart classes resulting from this study, the adult-ectognathate mouthpart class has the most highly structured subclustering patterns and the most diverse assemblage of taxa. At the level of the present analysis, 19 basic clusters are identified. However, the broad patterns by which subclusters aggregate should be noted. First, there is an approximately even division of the adult-ectognathate cluster into two groups of subclusters (see insets of Fig. 36a to 36g). The left-hand half of the cluster is essentially orthopteroid (or polyneopterous) in character whereas the right-hand half is entirely coleopteran except for the single case of an isolated isopteran (see Table 1 for terminology). These two groups subdivide the cluster rather evenly: the orthopteroid group has nine subclusters and 157 taxa whereas the coleopteran group has 10 subclusters and 133 taxa. Within the orthopteroid group subclustering patterns map onto taxonomic

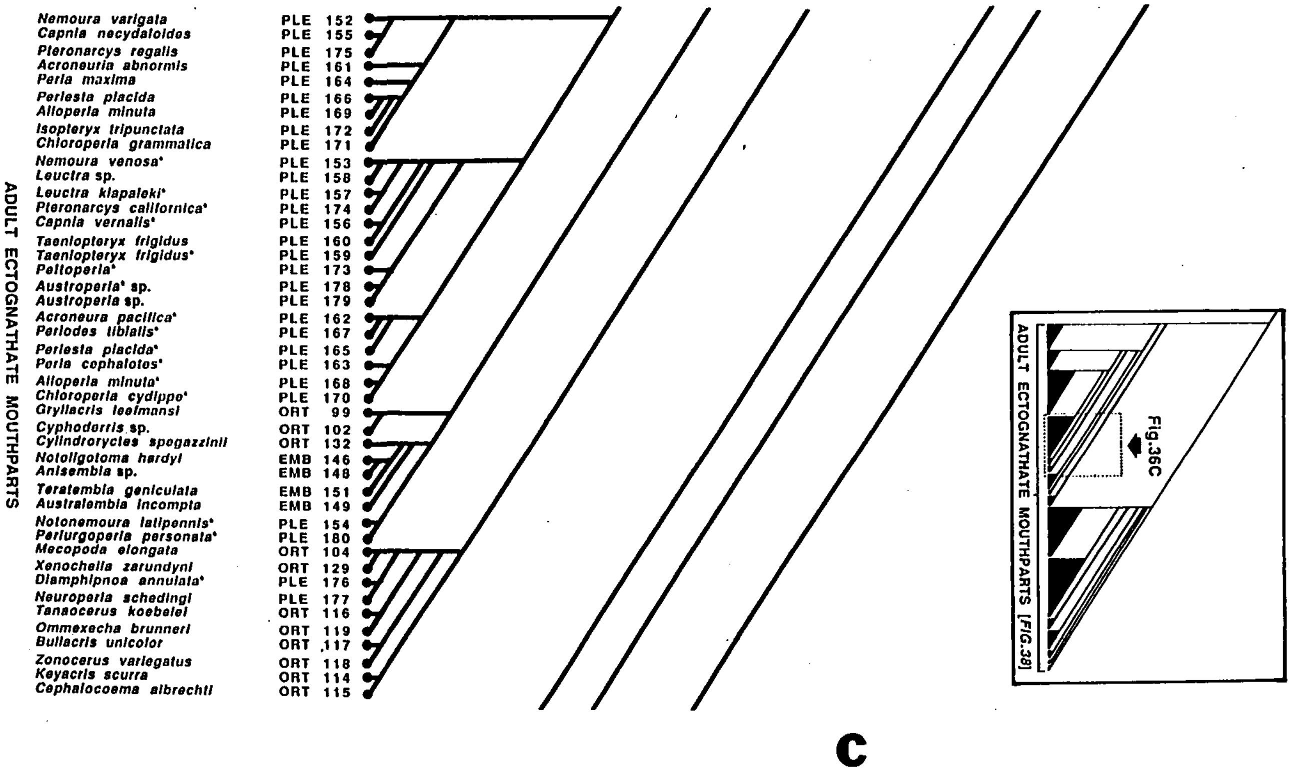
FIGURE 36. Cluster analysis dendrogram of taxa comprising the Adult Ectognathate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

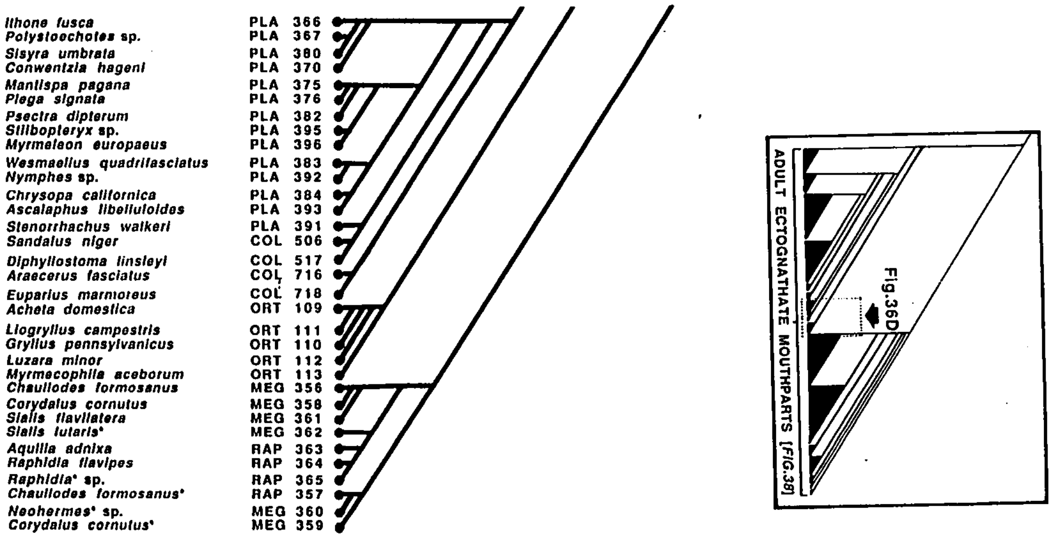

Tricholepidon gertschi TYN 18
Zorotypus hubbardi ZOR 181
Acrotelsa collaris TYN 19
Ctenolepisma longicaudata TYN 20
Lepisma sp. TYN 21
Thermobia domestica TYN 22
Protrinemura mediterranea TYN 23
Macroxyela sp. HYM1229
Xyela minor HYM1231
Hoplocampa halcyon HYM1239
Macrophya pluricincta HYM1240
Pristiphora erichsonii HYM1242
Apanteles golmeratus HYM1255
Bathyaulax alami HYM1256
Pelecinus sp. HYM1270
Gasteruption jaculator HYM1268
Apozyx penyai HYM1264
Pseudogonalys hahni HYM1265
Heterobathmia pseuderiacrania LEP 1088
Micropteryx calthella LEP 1090
Palaeomicroides fasciatella LEP 1093
Sabatinca auruncella LEP 1094
Mnemonica auricyanea LEP 1092
Agathiphaga vitiensis LEP 1096
Cryptocerus punctulatus BLA 74
Blaberus cranifer BLA 79
Blatta orientalis BLA 75
Periplaneta australasiae BLA 76
Blatella germanica BLA 77
Parcoblatta pensylvanica BLA 78
Mastotermes darwinensis ISO 84
Rhinotermes taurus ISO 89
Odontotermes obesus [soldier] ISO 93
Nasutitermes chaquimayensis ISO 92
Odontotermes obesus [worker] ISO 94
Kalotermes flavicollis ISO 85
Archotermopsis sp. ISO 86
Odontotermes obesus [drone] ISO 95
Termposis sp. ISO 87
Zootermposis angusticollis ISO 88
Macrotermes gilvus ISO 91
Fig.36A
ADULT ECTOGNATHATE MOUTHPARTS [FIG.38]

a

ADULT ECTOGNATHATE MOUTHPARTS


Stenopelmatus sp. ORT 97
Locusta migratoria ORT 125
Tachycines asynamorus ORT 101
Amblycorypha oblongifolia ORT 103
Orchelimum vulgare ORT 107
Saga serrata ORT 106
Decticus albifrons ORT 105
Schistocera gregaria ORT 127
Romalea microptera ORT 120
Melanopus differentialis ORT 126
Dissosteira carolina ORT 123
Marellia remipes ORT 121
Anacrydium aegyptium ORT 122
Hippiscus sp. ORT 124
Tetrix arenosus ORT 130
Tridactylis apicalis ORT 131
Tryxalis nasuta ORT 128
Macropathus filifer ORT 100
Grylloblatta campodeiformis GRY 96
Gryllotalpa gryllotalpa ORT 108
Embia ramburi EMB 145
Oligotoma hospes EMB 150
Embolyntha batesi EMB 147
Timema sp. PHA 133
Anisomorpha ferruginea PHA 134
Phryganistra virgea PHA 138
Carausius morosus PHA 137
Necrosia sparaxes PHA 135
Diaphanomera femorata PHA 136
Echinosoma afrum DER 139
Anisolabis maritima DER 140
Forficula auricularia DER 142
Labidura riparia DER 141
Arixenia esau DER 144
Hemimerus talpoides DER 143
Eremiaphila sp. MAN 80
Tenodera sinensis MAN 83
Mantis religiosa MAN 81
Stagnomantis carolina MAN 82
ADULT ECTOGNATHATE MOUTHPARTS
Fig.36B
ADULT ECTOGNATHATE MOUTHPARTS [FIG.38]
b


Nemoura varigata PLE 152
Capnia necydaloides PLE 155
Pteronarcys regalis PLE 175
Acroneuria abnormis PLE 161
Perla maxima PLE 164
Perlesta placida PLE 166
Alloperla minuta PLE 169
Isopteryx tripunctata PLE 172
Chloroperla grammatica PLE 171
Nemoura venosa* PLE 153
Leuctra sp. PLE 158
Leuctra klapaleki* PLE 157
Pteronarcys californica* PLE 174
Capnia vernalis* PLE 156
Taeniopteryx frigidus PLE 160
Taeniopteryx frigidus* PLE 159
Peltoperla* PLE 173
Austroperla* sp. PLE 178
Austroperla sp. PLE 179
Acroneura pacifica* PLE 162
Perlodes tibialis* PLE 167
Perlesta placida* PLE 165
Perla cephalotes* PLE 163
Alloperla minuta* PLE 168
Chloroperla cydippe* PLE 170
Gryllacris leeimansi ORT 99
Cyphodorris sp. ORT 102
Cylindroryctes spegazzinii ORT 132
Notoligotoma hardyi EMB 146
Anisembia sp. EMB 148
Teratembia geniculata EMB 151
Australembia incompta EMB 149
Notonemoura latipennis* PLE 154
Perlurgoperla personata* PLE 180
Mecopoda elongata ORT 104
Xenocheila zarundyni ORT 129
Diamphipnoa annulata* PLE 176
Neuroperla schedingi PLE 177
Tanaocerus koebelei ORT 116
Ommexecha brunneri ORT 119
Bullacris unicolor ORT 117
Zonocerus variegatus ORT 118
Keyacris scurra ORT 114
Cephalocoema albrechti ORT 115
ADULT ECTOGNATHATE MOUTHPARTS
Fig.36C
ADULT ECTOGNATHATE MOUTHPARTS [FIG.38]
C


Ithone fusca PLA 366
Polystoechotes sp. PLA 367
Sisyra umbrata PLA 380
Conwentzia hageni PLA 370
Mantispa pagana PLA 375
Plega signata PLA 376
Psectra dipterum PLA 382
Stilbopteryx sp. PLA 395
Myrmeleon europaeus PLA 396
Wesmaelius quadrifasciatus PLA 383
Nymphes sp. PLA 392
Chrysopa californica PLA 384
Ascalaphus libelluloides PLA 393
Stenorrhachus walkeri PLA 391
Sandalus niger COL 506
Diphyllostoma linsleyi COL 517
Araecerus fasciatus COL 716
Euparius marmoreus COL 718
Acheta domestica ORT 109
Liogryllus campestris ORT 111
Gryllus pennsylvanicus ORT 110
Luzara minor ORT 112
Myrmecophila aceborum ORT 113
Chauliodes formosanus MEG 356
Corydalus cornutus MEG 358
Sialis flavilatera MEG 361
Sialis lutaria* MEG 362
Agulla adnixa RAP 363
Raphidia flavipes RAP 364
Raphidia* sp. RAP 365
Chauliodes formosanus* RAP 357
Neohermes* sp. MEG 360
Corydalus cornutus* MEG 359
Fig.36D
ADULT ECTOGNATHATE MOUTHPARTS [FIG.38]

ADULT ECTOGNATHATE MOUTHPARTS

d

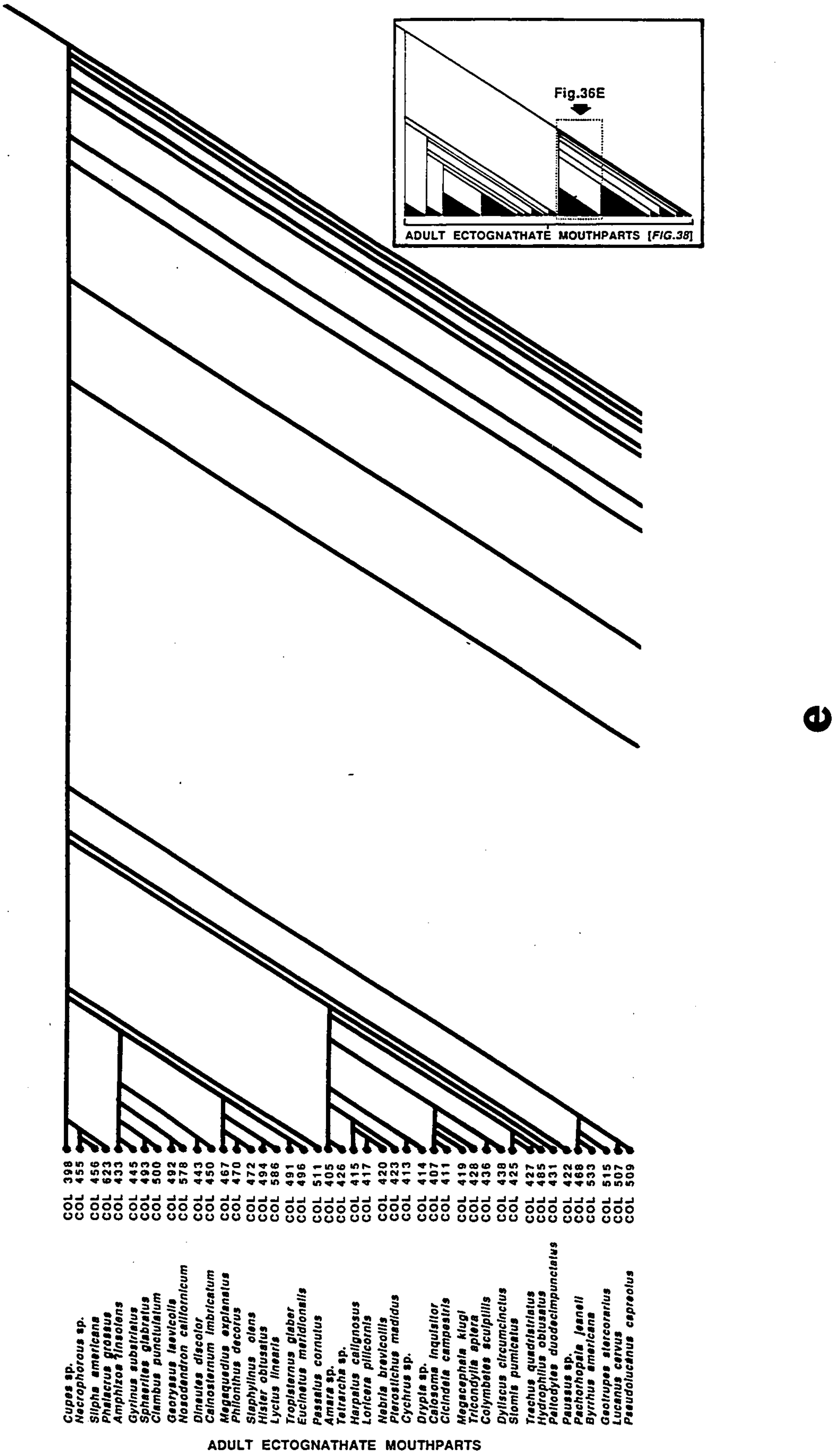
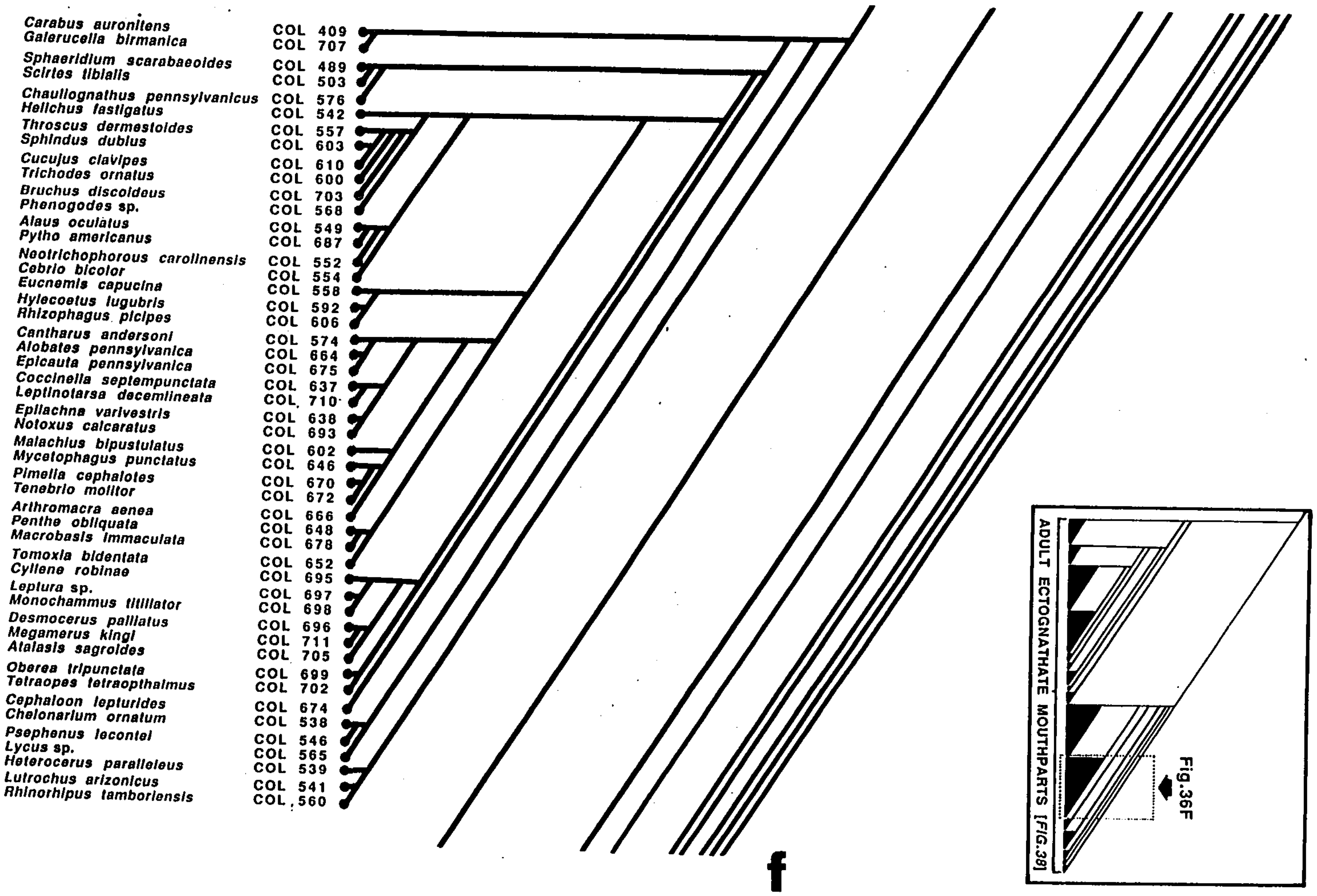
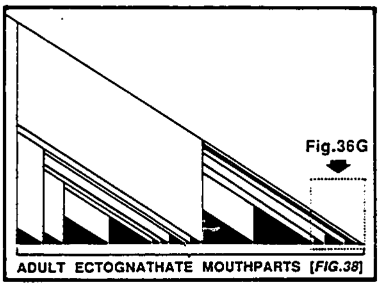
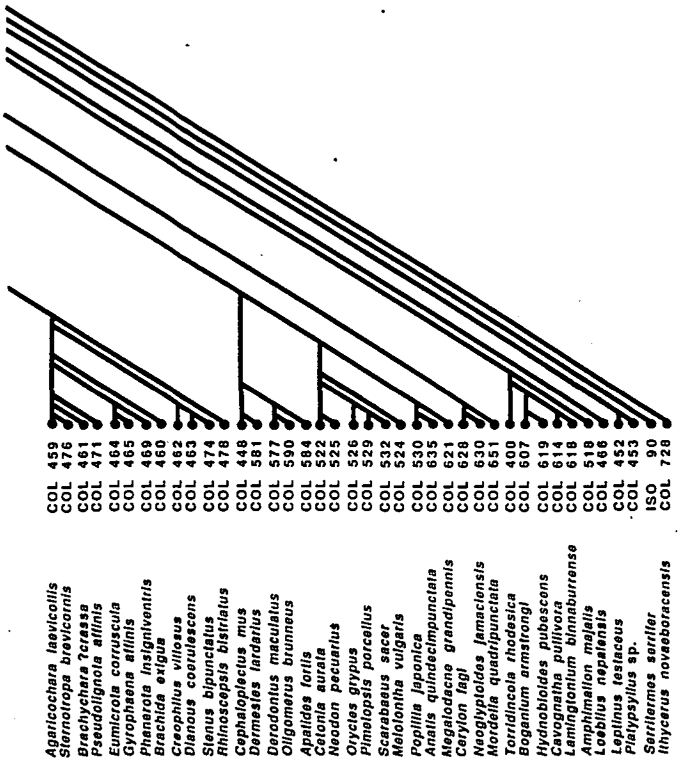


Fig.36E
ADULT ECTOGNATHATE MOUTHPARTS [FIG.38]
e
COL 398 Cupes sp.
COL 455 Necrophorous sp.
COL 456 Silpha americana
COL 623 Phalacrus grossus
COL 433 Amphizoa insolens
COL 445 Gyrinus substriatus
COL 493 Sphaerites glabratus
COL 500 Clambus punctulatum
COL 492 Georyssus laevicollis
COL 578 Nosodendron californicum
COL 443 Dineutes discolor
COL 450 Cainosternum imbricatum
COL 467 Megaquedius explanatus
COL 470 Philonthus decorus
COL 472 Staphylinus olens
COL 494 Hister obtusatus
COL 586 Lycus linearis
COL 491 Tropisternus glaber
COL 496 Eucinetus meridionalis
COL 511 Passalus cornutus
COL 405 Amara sp.
COL 426 Tetrarcha sp.
COL 415 Harpalus caliginosus
COL 417 Loricera pilicornis
COL 420 Nebria brevicollis
COL 423 Pterostichus madidus
COL 413 Cychrus sp.
COL 414 Drypta sp.
COL 407 Calosoma inquisitor
COL 411 Cicindela campestris
COL 419 Megacephala klugi
COL 428 Tricondylla aptera
COL 436 Colymbetes sculptilis
COL 438 Dytiscus circumcinctus
COL 425 Siomis pumicatus
COL 427 Trechus quadristriatus
COL 485 Hydrophilus obtusatus
COL 431 Peltodytes duodecimpunctatus
COL 422 Paussus sp.
COL 468 Pachorhopala jeanelli
COL 533 Byrrhus americana
COL 515 Geotrupes stercorarius
COL 507 Lucanus cervus
COL 509 Pseudolucanus capreolus
ADULT ECTOGNATHATE MOUTHPARTS


Carabus auronitens COL 409
Galerucella birmanica COL 707
Sphaeridium scarabaeoides COL 489
Scirtes tibialis COL 503
Chauliognathus pennsylvanicus COL 576
Helichus fastigatus COL 542
Throscus dermestoides COL 557
Sphindus dubius COL 603
Cucujus clavipes COL 610
Trichodes ornatus COL 600
Bruchus discoideus COL 703
Phenogodes sp. COL 568
Alaus oculatus COL 549
Pytho americanus COL 687
Neotrichophorous carolinensis COL 552
Cebrio bicolor COL 554
Eucnemis capucina COL 558
Hylecoetus lugubris COL 592
Rhizophagus picipes COL 606
Cantharus andersoni COL 574
Alobates pennsylvanica COL 664
Epicauta pennsylvanica COL 675
Coccinella septempunctata COL 637
Leptinotarsa decemlineata COL 710
Epilachna varivestris COL 638
Notoxus calcaratus COL 693
Malachius bipustulatus COL 602
Mycetophagus punctatus COL 646
Pimelia cephalotes COL 670
Tenebrio molitor COL 672
Arthromacra aenea COL 666
Penthe obliquata COL 648
Macrobasis immaculata COL 678
Tomoxia bidentata COL 652
Cyllene robinae COL 695
Leptura sp. COL 697
Monochammus titillator COL 698
Desmocerus palliatus COL 696
Megamerus kingi COL 711
Atalasis sagroides COL 705
Oberea tripunctata COL 699
Tetraopes tetraopthalmus COL 702
Cephaloon lepturides COL 674
Chelonarium ornatum COL 538
Psephenus lecontei COL 546
Lycus sp. COL 565
Heterocerus paralleleus COL 539
Lutrochus arizonicus COL 541
Rhinorhipus tamboriensis COL 560
f
Fig.36F
ADULT ECTOGNATHATE MOUTHPARTS [FIG.38]

ADULT ECTOGNATHATE MOUTHPARTS




Agaricochara laevicollis COL 459
Sternotropa brevicornis COL 476
Brachychara ?crassa COL 461
Pseudoligncta affinis COL 471
Eumicrota corruscula COL 464
Gyrophaena affinis COL 465
Phanerota insigniventris COL 469
Brachida exigua COL 460
Creophilus villosus COL 462
Dianous coerulescens COL 463
Stenus bipunctatus COL 474
Rhinoscepsis bistriatus COL 478
Cephaloplectus mus COL 448
Dermestes lardarius COL 581
Derodontus maculatus COL 577
Oligomerus brunneus COL 590
Apatides fortis COL 584
Cetonia aurata COL 522
Neodon pecuarius COL 525
Oryctes grypus COL 526
Pimelopsis porcellus COL 529
Scarabaeus sacer COL 532
Melolontha vulgaris COL 524
Popillia japonica COL 530
Anatis quindecimpunctata COL 635
Megalodacne grandipennis COL 621
Cerylon fagi COL 628
Neoglyptoides jamaciensis COL 630
Mordella quadripunctata COL 651
Torridincola rhodesica COL 400
Boganium armstrongi COL 607
Hydnobioides pubescens COL 619
Cavognatha pullivora COL 614
Lamingtonium binnaburrense COL 618
Amphimallon majalis COL 518
Loeblius nepalensis COL 466
Leptinus testaceus COL 452
Platypsyllus sp. COL 453
Serritermes serrifer ISO 90
Ithycerus novaeboracensis COL 728

ADULT ECTOGNATHATE MOUTHPARTS

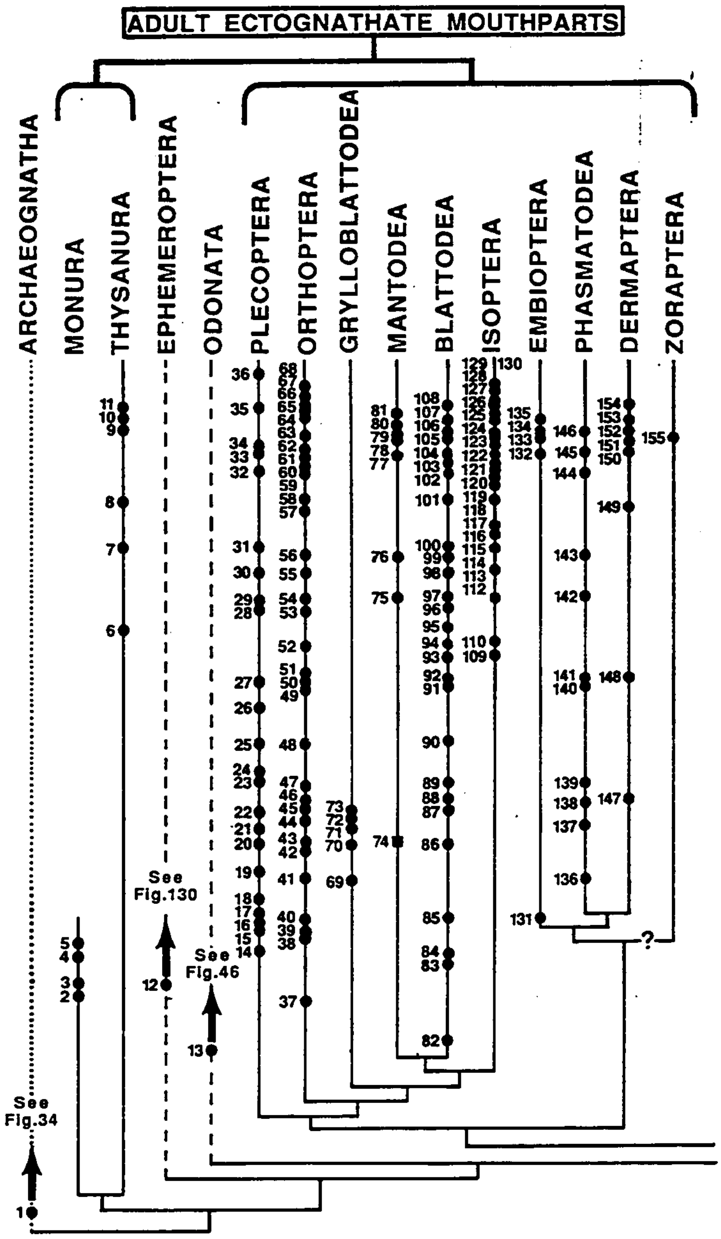
compositions at the ordinal level in many instances. In other cases taxa of structurally heterogenous orders, such as Orthoptera, Plecoptera and possibly Embioptera are split between two or more subclusters. For the coleopteran group there are two major characterizations of subclusters. Several subclusters represent eclectic assemblages of taxa from several families from often two or even three suborders. A greater number of subclusters have taxonomically restrictive memberships and include only a single family or an evolutionarily close suite of families in the same superfamily or in related superfamilies. It is conceivable that these two groups of subclusters each warrant mouthpart class status. I opted for consolidating them because of the significantly long branch-length of adult-ectognathates when compared to other such clusters (Fig. 28).

Within the orthopteroid group of clusters, Subcluster 1 (bracketed by data-set nos. 18 to 1096 of Fig. 36a) consists of a thysanuran and zorapteran group, a symphytan and parasitican hymenopteran group and a zeuglopteran lepidopteran group. These three groups exhibit similarities in head-related and general mouthpart features but differ in specific features of the mouthpart elements. Subcluster 2 (data-set nos. 74 to 91 of Fig. 36a) is less diverse and consists of blattodean and isopteran groups. Both groups exhibit close similarities in general mouthpart features and most mouthpart element details, differing only in a few characters of mandible shape and glossal and paraglossal modification. Subcluster 3 (97 to 82 of Fig. 36b) is a diverse assemblage of 39 taxa from 6 orders, namely orthopterans, a grylloblattid, embiopterans, phasmatodeans, dermapterans and a mantodean. Significantly there is not a partitioning of this subcluster along ordinal lines. This sharing of taxa of the same order in different groupings is based on only several characters of the maxilla and labium. Subcluster 4 (152 to 170 of Fig. 36c) is a similarly diverse suite, consisting of 25 taxa of adult and immature plecopterans. Although plecopteran immatures are aquatic naiads that have significantly different diets than their adults, the presence of both life-stages in the same subcluster indicates that the adult/naiad dichotomy is more similar to raptorial ectognathates (Section 8.4.7) than to pectinates and their adult stages (Sections 8.3.11 and 8.10.3). Subcluster 5 (99 to 180 of Fig. 36c) encompasses nine taxa of orthopterans, embiopterans and plecopterans. Although most orthopteran taxa are located in Subclusters 3 and 6, the Gryllacrididae, Haglidae and Cylindrachetidae bear mouthparts that are sufficiently aberrant that they are more phenetically close to poorly known embiopterans and notonemourid and gripopterygid plecopterans. Subcluster 6 (104 to 115 of Fig. 36c) incorporates caeliferan orthopterans and the archaic plecopteran family Eustheniidae. Subcluster 7 (366 to 718 of Fig. 36d) comprises three coleopteran taxa from the superfamilies Dascilloidea, Scarabaeoidea and Curculionoidea and all planipennian adults except for the Nemopteridae. The absence of adult nemopterids is significant since their highly divergent mouthparts are accomodated in the rostrate and glossate classes (Sections 8.3.9 and 8.7.2). Subcluster 8 (109 to 113 of Fig. 36d) consists of grylloid orthopterans (crickets). This well-integrated subcluster is attributable to characters describing the enlargement of the hypopharynx and adjacent structures into an adsorptive organ convergent with the haustorium of haustoriates or labellum of labellates. Subcluster 9 (356 to 359 of Fig. 36d) constitutes adult and larval megalopterans and raphidiopterans. The discreteness between adult and immature stages in this subcluster is not as pronounced as it is for Subcluster 4 or between adult-ectognathates and larval-ectognathates.

Among the coleopteran group of subclusters, Subcluster 10 (398 to 509 of Fig. 36e) is a diverse assemblage of 44 taxa comprising three suborders, 10 superfamilies and 20 families of coleopterans. Together with Subcluster 11, they comprise the overwhelming bulk of coleopteran diversity within adult ectognathates. Members of Subcluster 10 are dominated by adephagans and plesiomorphic polyphagans and possess prognathous mouthparts, falcate and prominent mandibles and are either predatory on insects or associated with wood. By contrast, Subcluster 11 (409 to 560 of Fig. 36f) consists of almost entirely apomorphic polyphagans with hypognathous mouthparts, tetragonal mandibles modified for vegetarianism and consume a variety of live tissues in terrestrial vascular plants and fungi. Many are obligate pollinivores or engage in fungal/tree/insect symbioses. The trend described in Subclusters 10 and 11 is not a new one; entomologists have previously noted this transition from predatory forms in the Adephaga and plesiomorphic Polyphaga to plant-feeding forms in apomorphic Polyphaga (Balduf 1935, Crowson 1981). Subclusters 12 to 19 are interpreted as peripheral to the central tendency exhibited in subclusters 10 and 11. Subcluster 12 (459 to 478 of Fig. 36g) comprises only staphylinids and a related pselaphid. Subcluster 13 (448 to 651 of Fig. 36g) incorporates eight families of staphylinoids, scarabaeoids, dermestoids, bostrichoids and cucujoids and apparently represents forms that are predaceous or wood-borers. Subcluster 14 (628 to 651 of Fig. 36g) are floricolous forms of the Cerylonidae and Mordellidae. Subcluster 15 (400 to 518 of Fig. 36g) is an assortment of mostly rare, recently described cucujoid families with adaptations to spore-feeding. Subcluster 16 (466 of Fig. 36g) is a structurally isolated staphylinid whereas taxa of Subcluster 17 (452 and 453 of Fig. 36g) are staphylinoids of the families Leptinidae and Platypsyllidae that are ectoparasitic on mammals and bear highly modified mouthparts. Lastly, Subclusters 18 (90 of Fig. 36g), a serritermitid isopteran and 19 (728 of Fig. 36g) an ithycerid curculionoid, are anomalous, isolated taxa.

Geochronologic History. By the Early Pennsylvanian Namurian B Stage (about 320Ma), adult-ectognathates were already a major component of the insect fauna. Deposits of this interval contain fossils of mostly extinct but also a few extant orders of paleopterans and generalized orthopteroid insects (Sharov 1971, Zessin 1987) including the diverse, extinct palaeodictyopteroids, who bore stylate mouthparts. These early adult-ectognathate forms probably included the orders Protorthoptera, Miomoptera, Protoblattodea (Crowson et al. 1967, Burnham 1983, Carpenter and Burnham 1985) and several small probable true orthopterans and blattodeans (Zeuner 1939, Crowson et al. 1967, Gorokhov 1987). Additional, anecdotal evidence supporting the presence of adult-ectognathates during this time are several reports from scalloped or otherwise excised pinnules and fronds from a diversity of Late Carboniferous plant groups that are found in compression floras, suggesting external foilage feeding (Van Ameron 1966, Van Ameron and Boersma 1971, Muller 1982, Scott and Taylor 1983, Labandeira and Beall 1990). Moreover, supplementary evidence is provided by a rich and varied suite of coprolites of various digested plant tissues in Late Carboniferous coal balls from the Illinois Basion of the Euramerican Continent (Rothwell and Scott 1983, 1988; Labandeira and Beall 1990). These data collectively indicate an early wave of adult-ectognathates occurring in forested lowland ecosystems of the Late Carboniferous. (See Fig. 37 for a phylogram summary of adult-ectognathates.)

During the Permian a second wave of adult-ectognathates appeared, consisting of holdovers from the Carboniferous as well as a new occurrences of adult holometabolans. Several rich insect faunas from the US [90], USSR [89,88,86], Czechoslovakia [92] and Australia [83] have revealed a highly diverse fauna of extinct and extant orders (Carpenter 1977) of adult-ectognathates, including thysanurans, blattodeans, caloneurodeans, miomopterans, orthopterans, embiopterans, plecopterans, protelytropterans, coleopterans, planipennians, raphidiopterans, megalopterans and glosselytrodeans (Ponomarenko 1969, Rohdendorf and Rasnitsyn 1980, Carpenter and Burnham 1985). Many taxonomically smaller, nonholometabolous groups, such as grylloblattodeans, mantodeans, isopterans, phasmatodeans, dermapterans and zorapterans appear later during the Early to Middle Mesozoic, although cladistic evidence indicates that most of these groups should have been present during the Permian. Ecological evidence for the presence of adult-ectognathates includes scalloped pinnule margins from *Glossopteris* floras from South


ADULT ECTOGNATHATE MOUTHPARTS
ARCHAEOGNATHA
MONURA
THYSANURA
EPHEMEROPTERA
ODONATA
PLECOPTERA
ORTHOPTERA
GRYLLOBLATTODEA
MANTODEA
BLATTODEA
ISOPTERA
EMBIOPTERA
PHASMATODEA
DERMAPTERA
ZORAPTERA
See Fig.34
See Fig.130
See Fig.46
?

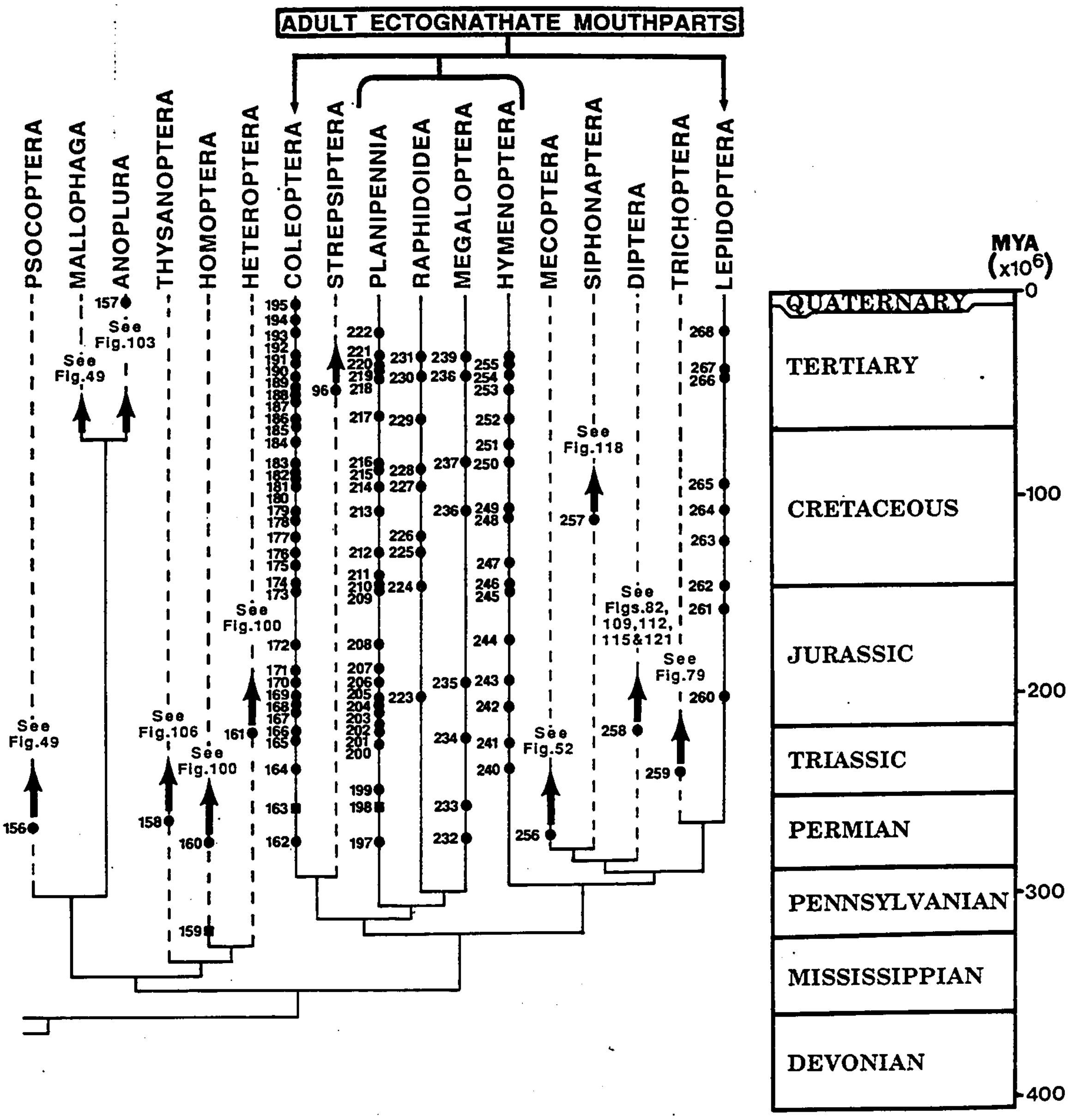


FIGURE 37. Geochronologic history of the Adult Ectognathate Mouthpart Class. See Appendix F for taxa, localities, and references corresponding to each fossil occurrence. The phylogram is after Kristensen (1981), Hennig (1981), Boudreaux (1987) and especially Jamieson (1987). The taxonomic level of analysis is the order. The outgroup is Archaeognatha. For the Hymenoptera and Lepidoptera, only adult ectognathate members have been plotted. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.

Africa and India (Plumstead 1963, Srivastava 1987). These insect-mediated feeding marks are consistent with a phytophagous orthopteroid insect as the causative agent. Additionally, coleopterans commenced their evolutionary diversification during the Permian and from a few well-studied forms there appears to be an association between archostemmatan cupedid beetles and wood-boring in loose-bark habitats (Crowson 1976, 1981; Hamilton 1978). This may indicate early durophagous specialization in adult-ectognathates.

The third and last major wave of adult-ectognathates occurred during the Early to Middle Mesozoic with the diversification of various mandibulate groups, such as several orthopteroid groups during the early part of the era, xyeloid hymenopterans during the Late Triassic [82] (Rasnitsyn 1964, 1975), plesiomorphic polyphagan coleopterans during the Early to Middle Jurassic [69,61,60] (Arnoldi et al. 1977, Crowson 1981) and zeuglopteran lepidopterans during the Lower Jurassic [69] (Whalley 1985, 1986). In many of these groups more advanced adult members forsook ectognathate mouthparts and solid-feeding for various mouthparts involved in fluid-feeding. The adults of several of these groups became dominant consumers of live tissues on vascular land plants, as indicated by cladistic analyses of modern phytophagous representatives and the fossil record. Others specialized in weakly-tuned coevolutionary relationships with flowering plants and received their nutriment dominately by pollen-feeding (Gottesburger 1977, 1988; Crepet and Friis 1987). Although adult coleopterans are generally implicated in this dietary shift, Krassilov and Rasnitsyn (1982) have paleontological evidence that symphytan hymenopterans also participated in the use of pollen as a food source during the Middle Mesozoic. It is also likely that micropterygid and other plesiomorphic lepidopterans were also concurrent pollinivores since many extant members consume pollen (Faegri and van der Pijl 1980, Barth 1985).

Previous Designations. Recognition of adult ectognathate mouthparts probably extends to Aristotle's *De Partibus Animalium*. Since they were considered the "most basic" of mouthpart types, structural equivalents of adult ectognathates were mentioned or discussed by Fabricius (1775, 1779), MacLeay (1821), Kirby and Spence (1826) and Latreille (1832). In these treatments frequently the adjective "biting" substituted for what is now commonly understood as "chewing."

Within modern times, the term "mandibulate" (e.g. Borror et al. 1976) or some variation thereof, such as "chewing type" (Metcalf 1929, Metcalf et al. 1962), "orthopteran type" (James and Harwood 1969), or "cutting and chewing" (Smith 1985), all have been used to refer to the mouthparts of most insects herein assigned to the Mandibulate Series. However, the Adult Ectognathate Class, as currently defined, is a more restrictive structural group and the above terms are applicable only in the broadest sense (see Table 6 for details).

Frequently, discussions and illustrations of the generalized mouthpart and head groundplan of pterygotes approach that of what is herein conceived as adult-ectognathate. Examples are "the definitive insect head" of Snodgrass (1935), the "generalized pterygote insect" of DuPorte (1977), or the "basic chewing type" of Arnett and Jacques

(1985). Most of these and similar designations are used in an archetypal sense and are idealized abstractions without reference to existant species. Since other mandibulate mouthpart classes exhibit significant structural deviations from adult-ectognathates, it may be appropriate to equate the above idealized descriptions loosely with the Adult Ectognathate Class. The closest expression of synonymy with adult-ectognathate mouthparts is provided by Denis and Bitsch (1973), who stated, with respect to their *appareil buccal broyeur*, the following mouthpart subtype:

> Les mandibules sont bien développés, maxille et labium ont typiquement une structure généralisée. Les Thysanoures et presque tous les Ptérygotes "inferieurs", ainse que les Coléoptères, Névroptères, les larves de Trichoptères et de Lépidoptères possèdent le plus souvent un appareil buccal de ce type (Denis and Bitsch 1973, p.40).

They consider mouthparts of mecopterans (rostrates, Section 8.3.9) and curculionoids (rhynchophorates, Section 8.3.10) as qualitatively different subgroupings within their "*appareil buccal broyeur*." This designation was elaborated by Chaudonneret (1982) who established a generalized biting-and-chewing insect as a ground plan (*théme*) for establishing *variations* in other structurally derived insect groups.

Because previous references to a generalized mandibulate mouthpart type have been couched in the formulation of archetypes or idealized abstractions, I am using the more concrete designation **adult-ectognathate** to designate the mouthpart class discussed herin. This term has no prior history of usage in the entomological literature.

Review of Literature. The literature on adult-ectognathate mouthparts is vast and detailed. In this section I will attempt to summarize briefly major works on the topic, recognizing that only a fraction of approximately 350 examined papers on adult-ectognathates will be mentioned. Of the total number of reference citations in this study, about 30% pertain to adult-ectognathates. Of these, the overwhelming majority involve studies of adult coleopteran mouthparts. I will first present a review of papers providing synoptic reviews of mouthpart structure for particular taxonomic groups. This will be followed by citation of important articles discussing mouthpart structure of particular species. Finally I will list studies focusing on structural variation of particular mouthpart elements.

Major illustrated summaries of orthopteroid mouthparts can be found in Yuasa (1920), Crampton (1921; 1932, head capsules only), Hoke (1924, plecopterans), Golden (1925), Walker (1933), and Strenger (1942), most of which discuss and illustrate representative taxa from several orders of insects. Reviews of neuropteroid mouthparts, especially coleopterans, can be found in Kadic (1902, labia), Pauly (1915, caraboids), Crampton (1921), Bertin (1923, scarabaeoids), Stickney (1923, head capsules), Verhoeff (1923), Williams (1938, maxillae and labia), Ferris (1942), Cook (1943, schematic diagrams), Dorsey (1943, schematic diagrams) and Forsythe (1982, 1983, with scanning electron micrographs). Bugnion (1930), Berland (1947) Gotwald (1969) and Bohart and Menke (1976) present mouthpart and head morphology data for many adult mandibulate hymenopterans.

Numerous individual works discuss and illustrate mouthpart and head structure of a single species, or a few selected species, frequently in exhaustive detail. A sampling of these studies include the following listing of mouthpart-focused descriptions of species from 17 adult ectognathate orders. For the Thysanura, the lepismatids *Lepisma saccharina* Linneaus has been described by Larink (1970) and Manton (1977) and *Thermobia domestica* (Packard) by Chaudonneret (1950). The archaic family Lepidotrichidae has a single relict form, *Tricholepidon gertschi* Wygodzinsky, described by Wygodzinski (1961).

Among orthopteroids, mouthpart and head structure has been described for orthopteran acridids, particularly *Xenocheila zarundnyi* Uvarov by Chapman (1966), and for *Dissosteira carolina* (Linneaus) by Snodgrass (1928). Other orthopterans from varied habitats include the generalized stenopelmatid, *Stenopelmatus* sp., treated by Crampton (1930a), a spelial raphidophorid, *Tachycines asynamorus* Adelmann by Wada (1965), the fossorial gryllotalpid *Gryllotalpa gryllotalpa* (Linneaus) by LaGreca (1939), and the semiaquatic pauliniid, *Marellia remipes* Uvarov by Carbonell (1959). Mouthpart structure for blattodeans has been described for blattids, namely *Periplaneta americana* (Linneaus) by Bugnion (1920) and Popham (1961), and the congeneric *P. australasiae* (Fabricius) by Mangan (1909). The recently discovered Grylloblattodea consists of a monotypic genus, the grylloblattid *Grylloblattodea campodeiformis* Walker, whose mouthparts have been described by Crampton (1926) and Walker (1931b, 1933, 1937). Within the Dermaptera, the mouthparts of the common forficulid earwig, *Forficula auricularia* Linneaus, has been described by Strenger (1949), Henson (1950) and Popham (1959). Other examined dermapterans include the labidurid, *Labidura riparia* Pallas, by Kadam (1961), and the parasitic forms *Arixenia esau* Jordan, an arixeniid, and *Hemimeris talpoides* Walker, an hemimerid, both described by Popham (1962a). Of the Mantodea, the mantid *Stagnomantis carolina* (Johannsen) was described by Leverreault (1936). Embiopterans are a generally neglected group in mouthpart morphology, but descriptions exist for the embiopterans *Embolyntha batesi* MacLachlan by Lacombe (1964), and for *Embia ramburi* Rimsky-Korsakow by Rahle (1970). Phasmatodeans have better coverage, with several families represented, including the heteronemid *Necrosia sparxes* Westwood by Gangrade (1965), the pseudophasmatid *Anisomorpha buprestoides* Stoller by Littig (1942), and the phasmatid *Carausius morosus* by Marquardt (1939). Mouthpart studies of isopterans have generally focused on comparative mandibular morphology based on intraspecific caste allometries, although Vishnoi (1956) describes all mouthpart structures for castes of the termitid *Odontotermes obesus* (Rambur).

Among adult neuropteroids, mouthpart and head descriptions are given for the corydalid megalopterans *Corydalus cornutus* (Linneaus) by Kelsey (1954), and *Chauliodes formosanus* Peterson by Maki (1936). Kramer (1955) described the mouthparts and head of the larva of *C. cornutus*. Mouthpart and head structures of *Sialis flavilatera* (Linneaus), a sialid, was described by Rober (1941). Raphidioideans are represented by the raphidiians *Raphidia flavipes* Stein described by Achtelig (1967), and *Agulla adnixa* (Hagen), described by Ferris and Pennebaker (1939) and Matsuda (1956). Descriptions of planipennian mouthparts are provided by Morse (1931) for the chrysopid *Chrysopa perla* Linneaus, and by Acker (1958) for the nemopterids *Stenorrhachis walkeri* (MacLachlan) and *Nemopterella* sp. Mouthparts and heads from many adult coleopteran groups have been documented, including notable studies by

Blackwelder (1936) for the staphylinid *Creophilus villosus* Gravenhorst; by Honomichl (1975) for the gyrinid *Gyrinus substriatus* Stephens; by Smith (1892a) for the scarabaeid *Copris carolina* Linneaus; by Pradhan (1939b) and Butt (1951) for the coccinellids *Coccinella septempunctata* (Linneaus) and *Epilachna varvivestris* Mulsant, respectively; by Campau (1940) for the cantharid *Chauliognathus pennsylvanicus* (DeGeer); and Khatib (1946) for the chrysomelid *Galerucella birmanica* (Jacoby).

Adult nonapoid hymenopterans, principally sawflies, are also a major contribution to adult-ectognathate mouthparts. Major studies of ectognathate hymenopteran mouthparts include the xyelid *Xyela minor* Norton by Berland (1947) and Snodgrass (1960), the tenthrediniids *Hoplocampa halcyon* Norton by Bird (1920) and Berland (1947) and *Macrophya pluricincta* Norton by Matsuda (1957), the braconids *Bathyaulax alami* Zaka-ur-Rab by Zaka-ur-Rab (1978) and *Apanteles gomeratus* (Linneaus) by Grandori (1911), the apozygid *Apozyx penyai* Mason by Mason (1971), the trigonalid *Pseudogonalys hahni* Spinola by Bugnion (1911) and the pelecinid *Pelecinus* sp. by Cresson (1887) and DuPorte (1946).

Individual mouthpart elements of adult-ectognathate mouthparts often have been discussed in the literature. They include mandibular form, mandibular dentition, labial and maxillary palp vestiture and sensory organelles, and clypeal and labral structures, among others. Mandibular form is best documented in isopterans, wherein mandibular shape, size and dentition has been used for phylogeny in the worker (Ahmad 1950) and soldier (Hare 1937) castes. Intraspecific mandibular variation has been investigated by Roonwal and Sengal (1960) in the worker caste of *Odontotermes obesus* (Rambur), and Deligne (1965) has interpreted mandibular shape and movement in terms of defensive behavorial strategies. Among coleopterans, mandibular form, and in part dentition, has been linked to boring into variously-indurated, solid substrates (Striganova 1967), to piercing prey (Witzke 1973), to various modes of cutting plant and animal tissue (Bertin 1923), to sweeping pollen (Fuchs 1974, Ashe 1984b) and to scraping dung (Hata and Edmunds 1983), among other functions.

The relevant features of mandibular dentition are cusp form and cusp position. Their relationship to diet type have been widely discussed for orthopterans and coleopterans. Important studies involving orthopterans include Nininger (1915), Golden (1925), Isely (1938, 1944), Gangwere (1960, 1964, 1965), Chapman (1964), Liebermann (1968), and Patterson (1983). For coleopterans, equally intensive investigations have been made by Pauly (1915), Bertin (1923), Golden (1925), Pradhan (1938), Butt (1951), and Osterwald (1954). Other studies of mandibular dentition have focused on blattodeans (Maiz and Hintze-Podufal 1979) and dermapterans (Popham 1959, 1962). The vestiture and sensory organelles of palpi are documented by Plateau (1885, maxillary), Blackwelder (1936, maxillary and labial), Thomas (1966, all appendages), Corbière (1967, all appendages), Blaney and Chapman (1970, maxillary), Roberts (1972, maxillary), Chapman and Thomas (1978, maxillary and labial), and Klein and Muller (1978, maxillary). Other mouthparts that are treated in depth include the epipharynx of scarabaeoids (Hayes 1928) and the clypeus and labium of various adult-ectognathate forms (Walker 1931a, Cook 1944a, Evans 1961).

THE UNIVERSITY OF CHICAGO

USE OF A PHENETIC ANALYSIS OF RECENT HEXAPOD MOUTHPARTS FOR THE DISTRIBUTION OF HEXAPOD FOOD RESOURCE GUILDS IN THE FOSSIL RECORD

VOLUME TWO

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE PHYSICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
DEPARTMENT OF GEOPHYSICAL SCIENCES

BY
CONRAD CHRISTOPHER LABANDEIRA

CHICAGO, ILLINOIS
AUGUST, 1990

8.3.5. Larval-Ectognathate Class (Class 4)

Description. Head quadrate, nonproboscate, generally retractile. Genae expanded dorsoventrally, comprising most of the cranial capsule; frontal region wide and triangular, with an inverted, Y-shaped epistomal suture. Gula present, minimal- to well-developed. Antennae filiform, less commonly papillate, palpiform or setaceous; stemmata present, mostly numerous, occasionally 2 or absent; compound eyes absent. Mouthparts mandibulate, prognathous or hypognathous, symmetrical or with single element asymmetry, nonprotractile.

Clypeus mostly transversely elongate, less commonly quadrate or absent; subsegmentation variable. Labrum vertically elongate, less commonly quadrate or absent; undivided; margin straight to shallowly curvilinear or pectinate. Hypopharynx variable; epipharynx mostly membranous but also lobate, setate or absent. Mandibles dicondylic; mostly tetragonal or falcate to less commonly palmate or rarely excavate; dentition variable; musculation of adduction/abduction. Maxilla with equant or elongate stipes; main body consisting of 2, rarely 3 or 4, sclerites; bearing a mala and palpus. Mala infrequently divided into a recognizable galea and lacinia. Maxillary palpus 4- to 3-segmented, rarely 2-segmented; mucronate or filiform-clavate, rarely papillate; short to intermediate in length. Galea fused to lacinia, bearing bristles mesially and raker-like structure distally; rarely otherwise. Labium with equant or elongate main-body divided into 2 or 3 segments; bearing a ligula and palps; ligula rarely divided into glossae and paraglossae. Labial palps mostly 2-segmented; filiform to uncommonly mucronate or papillate; short to intermediate in length. Glossae variable, often a generalized lingulate lobe; paraglossae absent. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. Several major features of the head and mouthparts separate larval-ectognathates from members of the six other terrestrial and aquatic larval mouthpart classes. An important feature of larval-ectognathates is the combination of a nonproboscate or otherwise unappendiculate, globose head and an epistomal suture subtending an inverted triangular sclerite on the anterior or anterodorsal aspect of the head capsule (variously termed the clypeofrons or frontoclypeal sclerite). Although members of the aquatic and larval mouthbrush and mandibulobrustiate mouthpart classes bear this characteristic triangular sclerite, mouthbrush members bear characteristic labral fans or other pectinate or penicillate mouthpart appendages, and mandibulobrustiates generally have an anteroposteriorally elongated head capsule, lack a galea and bear a labiohypopharyngeal spinneret (see Sections 8.3.12 and 8.3.13). Also, the head capsule of larval-ectognathates is typical of generalized holometabolous larvae and lacks the internal, posteriorly-directed apotomes or other processes found in sericterates (Section 8.3.14) or the tentorial arms originating from the cephalopharyngeal capsule of mouthhooks (Section 8.4.4)

The mandibles of larval-ectognathates are tetragonal, falcate or palmate, but lack major pectinate structures for filter feeding or sweeping, although they may bear small basal brushes. Although the mandibles are sometimes falcate, they never bear longitudinal gutters or a tubule originating subapically and debouching at the mandible base, as in members of the fossate-complex, tubulomandibulate and mouthhook mouthpart classes (Section 8.4). Larval-ectognathate mandibles articulate perpendicular to the body sagittal plane and thus occlude, unlike the nonocclusal articulation of mouthhook mandibles parallel to the body sagittal plane.

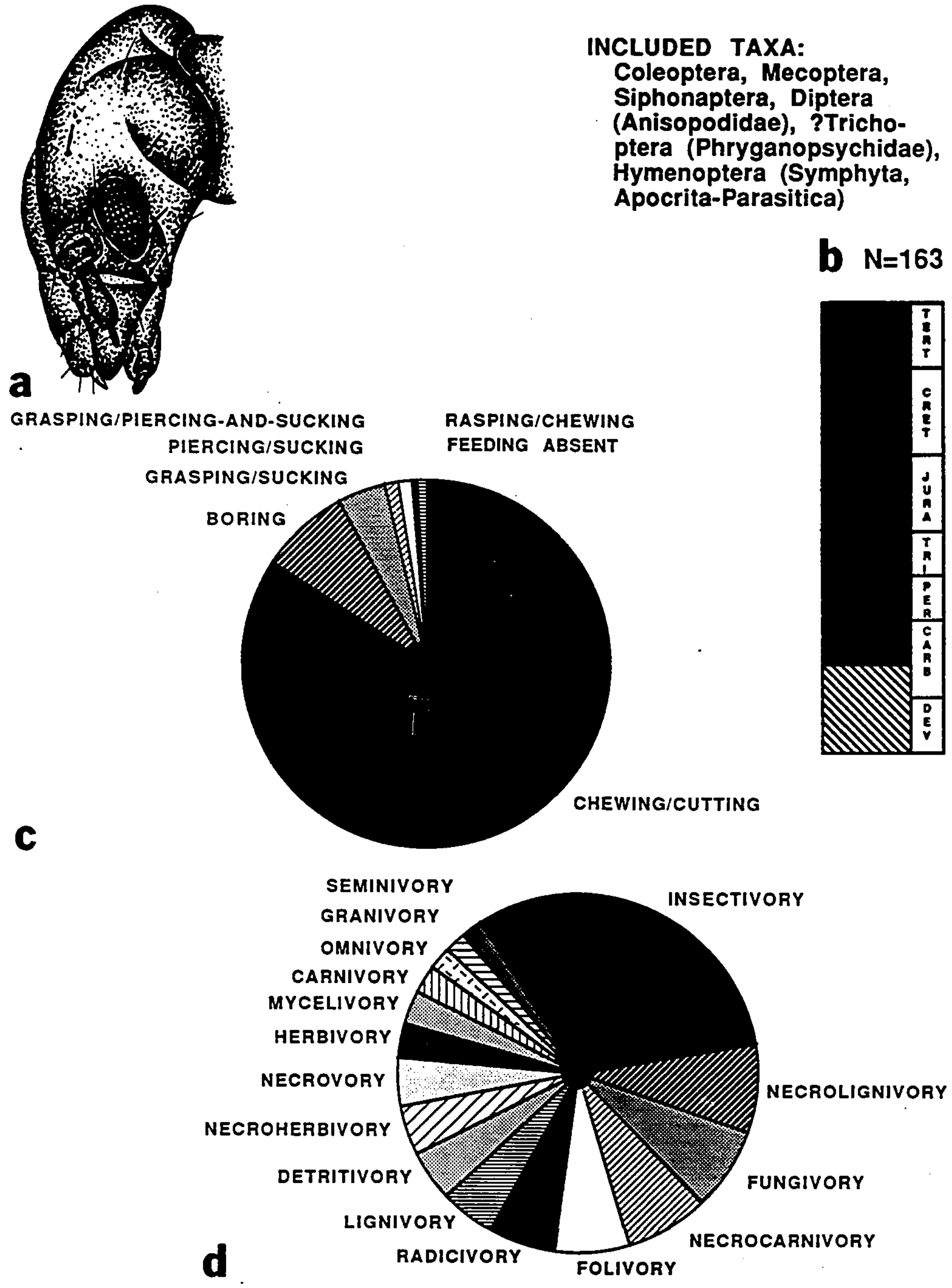
Larval-ectognathate maxillae consist of elements that are not structurally fused or otherwise connected to adjacent mouthpart regions. This condition differs significantly from the maxillolabiate complex of maxillolabiates (Section 8.3.6) or the various fusions between mandibular and maxillary sclerites of the mouthhook and mouthbrush classes. Additionally, the maxillary lacinia forms part of the generalized, lingulate, often bristle-bearing malar lobe and is not an elongate, scythe-shaped structure found in members of the fossate-complex.

The labium of larval-ectognathates is a generalized structure exhibiting abbreviation of many elements, but lacking the labiohypopharyngeal spinneret of mandibulobrustiates, sericterates and possibly reduced-trophics. Thus larval-ectognathates possess a lingulate or otherwise generalized ligula rather than a ligula modified into an elongate, duct-bearing spinneret. An associated labial feature is the presence of robust, usually two-segmented palps, unlike the aciculate or stubby palps associated with the labiohypopharyngeal spinneret of the three other mouthpart classes.

The larval-ectognathate mouthpart class can only be confused with mouthpart classes composed of holometabolous larvae. Cranial capsules of holometabolous larvae are found in mouthpart classes other than larval-ectognathates and they can be differentiated from larval-ectognathates by features of the mouthparts mentioned above. Because of the presence of generalized, unelaborated mouthpart elements and the lack of fusion between or among mouthpart regions, larval-ectognathates can be differentiated from all other, more specialized mouthpart classes containing aquatic or terrestrial larvae.

Diversity and Natural History. Members of the larval ectognathate moutpart class occur in virtually every terrestrial, freshwater and occasionally marine habitat and consume the entire spectrum of insect diets (Fig. 38). Larval-ectognathates are predatory carnivores on terrestrial and freshwater arthropods and other invertebrates; they inhabit the spatiotemporally restricted habitats of dung, carrion and fungi; and they consume the seed plant organs of roots, stems, leaves and reproductive structures (Fig. 38). They are have partitioned each of these plant organs according to tissue type. For example, stem consumers include wood-borers, bark "engravers," pith-miners, consumers of phloem and xylem and feeders on cambial tissue. For a sampling of the variety of diets possessed by larval-ectognathates, the reader is referred to Balduf (1935) and Johnson and Lyon (1976) for examples.

Larval-ectognathates comprise the larval stages of virtually all coleopterans, apparently all mecopterans and siphonapterans and a few plesiomorphic lepidopterans and dipterans. The degree of convergence among larval ectognathates is difficult to assess and is dependent on estimates of sister-group relationships among plesiomorphic holometabolous clades (see Fig. 40 for one version). For example, if the unique



INCLUDED TAXA:
Coleoptera, Mecoptera, Siphonaptera, Diptera (Anisopodidae), ?Trichoptera (Phryganopsychidae), Hymenoptera (Symphyta, Apocrita-Parasitica)

FIGURE 38. Overview of the Larval Ectognathate Mouthpart Class. a, *Panorpa communis** Linneaus (Mecoptera: Panorpidae, data-set no. 762), after Bierbrodt (1943); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

mouthparts of plannipenians (Section 8.4.2) were a derived condition from ancestors possessing larval-ectognathate mouthparts and if the larval mouthparts of megalopterans and raphidiopterans were also secondarily derived, then the most parsimonious (though not necessarily most likely) scenario for the orgin of larval-ectognathate mouthparts is that they are diphyletic. This scenario posits a origin in a Neuropteroidea + (Diptera + [Mecoptera + Siphonaptera]) clade and an origin in the Lepidoptera. A different scenario places an independent origin of larval ectognathates among the Coleoptera from a fossate-complex archetype and other separate derivations into Siphonaptera + Mecoptera, Diptera, and Lepidoptera clades, indicating a quadriphyletic origin of the mouthpart class. However, further research needs to be conducted on the basal synapomorphies of major holomeabolan clades (Köningsmann 1976, Hennig 1981, Kristensen 1981) to provide clarification of the above suggestions.

The fossil history of larval-ectognathates extends to the Late Carboniferous and conceivably to the Early Devonian (Fig. 40). During the transition from the Paleozoic insect fauna to the modern insect fauna during the Permian, the taxonomic diversity of larval-ectognathates must have risen dramatically. It is probable that by the Early Mesozoic they increased their proportional representation to the level of today. Currently larval-ectognathates have members from five orders, 167 families and approximately 313,000 species. Although they only represent 12% of the data-set they comprise about 22% of modern hexapods (Table 5, Fig. 131) when normalized to the taxonomic proportions of the extant hexapod fauna (Appendix D). This corresponds to a rank-order of

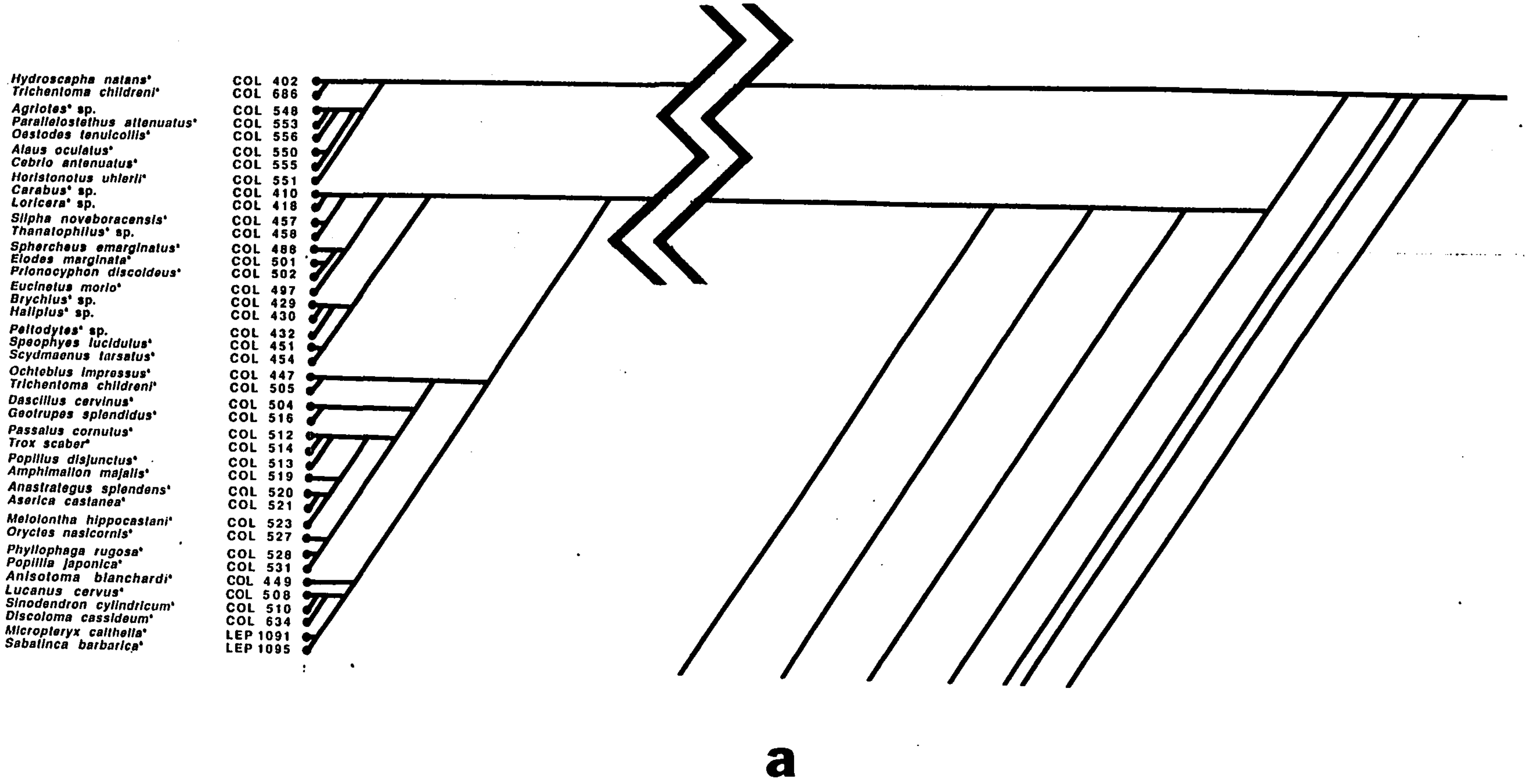
2 among the 34 mouthpart classes (Fig. 131). Alhough the scope of life-habits and dietary specializations of larval-ectognathates are too varied and numerous to recount here, I will provide only a brief sketch of their dietary breadth.

Among coleopterans, archostemmatans appear to be associated with bark or rotting wood (Hamilton 1978, Crowson 1981). Myxophagans are very small, cryptic forms that ingest filamentous algae and possibly fungal mycelia, often in aquatic habitats (Crowson 1981). Adephagan larvae are campodeiform and active, mobile predators in aquatic and terrestrial habitats that possess prominent, exserted heads which bear large, usually falcate mandibles. For primitive members of the Polyphaga, such as the Staphylinoidea and Hydrophiloidea, larval members are terrestrial or aquatic, predatory larvae; within the Eucinetoidea, Dascilloidea, Scarabaeoidea, Byrrhoidea, Dryopoidea, Elateroidea and Dermestoidea there is a trend toward feeding on detritus, carrion, roots and rotting wood but rarely green plant tissue. Buprestoids, Bostrichoids and Lymnexoids are wood-borers and range from taxa feeding on live wood to those occurring on highly decomposed logs. Most cleroids are predaceous and insectivorous. In the Cucujoidea, Tenebrionoidea, Chrysomeloidea and Curculionoidea the dominant trend is consumption of live plant and fungal tissues, including folivory, frugivory, sporivory/pollenivory, nectarivory, fresh wood, seeds, grain and roots; only infrequently are rotting tissues and insects consumed. The only significant carnivores or insectivores in these four superfamilies are members of the families Cucujidae, Colydiidae and Coccinellidae (Balduf 1935). Mecopteran larvae are scavengers or active predators (Richards and Davies 1977), though they avidly consume spores and pollen when given an opportunity (Malyshev 1968). Siphonapteran larvae consume shed dermal products and organic waste (Brues 1972), but rarely blood. Eriocranoid lepidopterans are browsers on moss or grass stems or possibly detritivores (Kristensen 1984b).

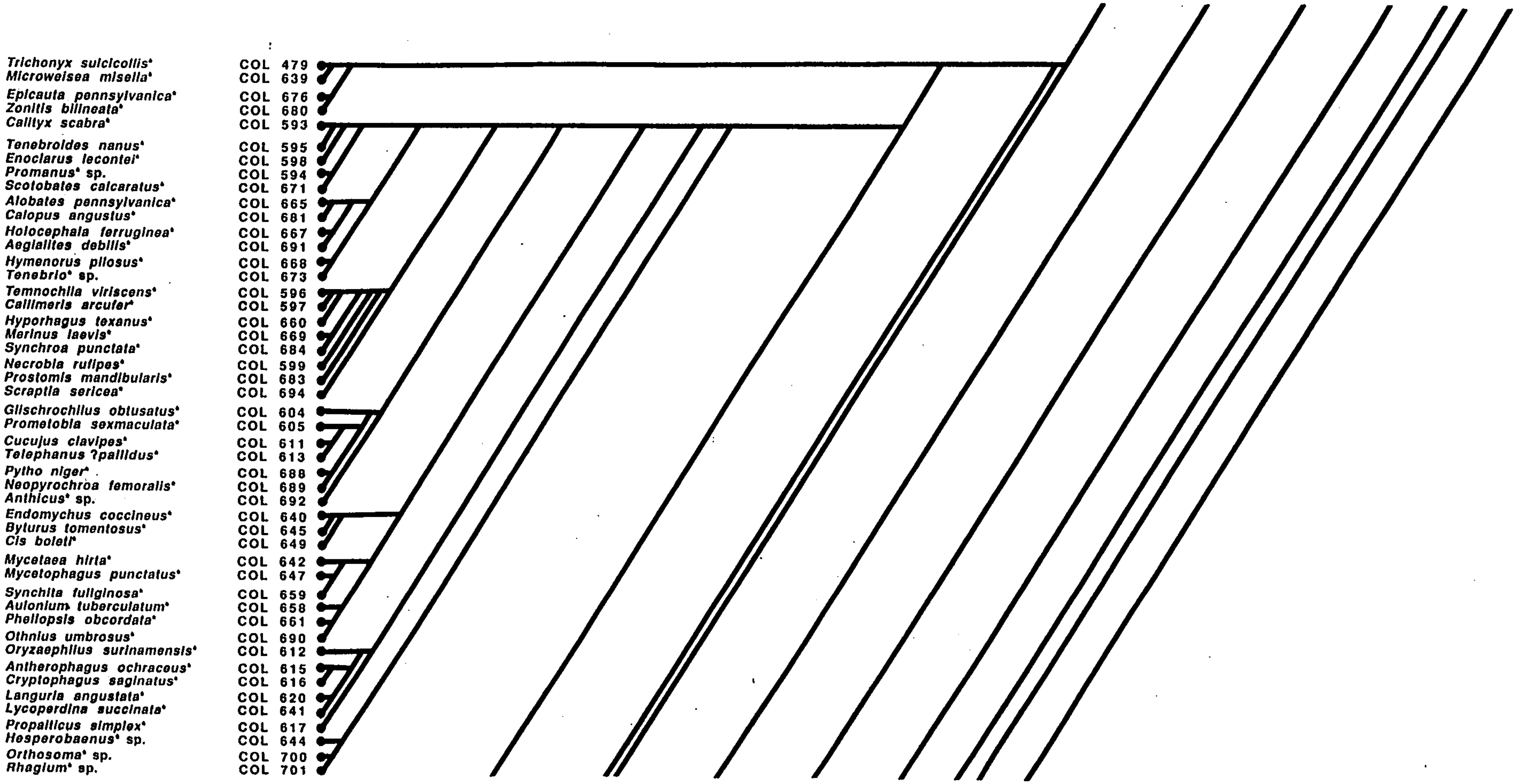
Structural Themes. The Larval Ectognathate Mouthpart class is interpreted to possess 13 discrete subclusters (Fig. 39). This mouthpart class presents a unique pattern in terms of scale (164 taxa) and the relatively long branch-lengths that separate highly homogenous clusters. This pattern indicates a high level of discreteness to the 13 subclusters of the cluster--a discreteness which often parallels taxonomic patterns and food utilization trends among several holometabolous orders and particularly within coleopterans. Phenetic differences among the subclusters are attributable to approximately 14 characters from predominately the clypeal/labral, mandibular, maxillary and labial mouthpart regions that have character-state distributions that isolate subclusters. Similarities among clusters and thus unity of the mouthpart class is indicated by relatively uniform and stable character-state distributions in the head region and aspects of overall mouthpart structure (see Appendix A).

Subcluster 1 (bracketed by data-set nos. 402 to 551 in Fig. 39) consists of a semiaquatic myxophagan hydroscaphid and, among the Polyphaga, the wireworm-like Trichentomidae and especially root-feeding wireworms of the Elateroidea (Elateridae, Cebrionidae). Of considerably greater diversity is Subcluster 2, comprising a broad spectrum of 17

FIGURE 39. Cluster analysis dendrogram of taxa comprising the Larval Ectognathate Mouthpart Class. Part A is vertically foreshortened, indicated by parallel ragged lines. See Fig. 28 for relationships of this mouthpart class to other mouthpart classes.

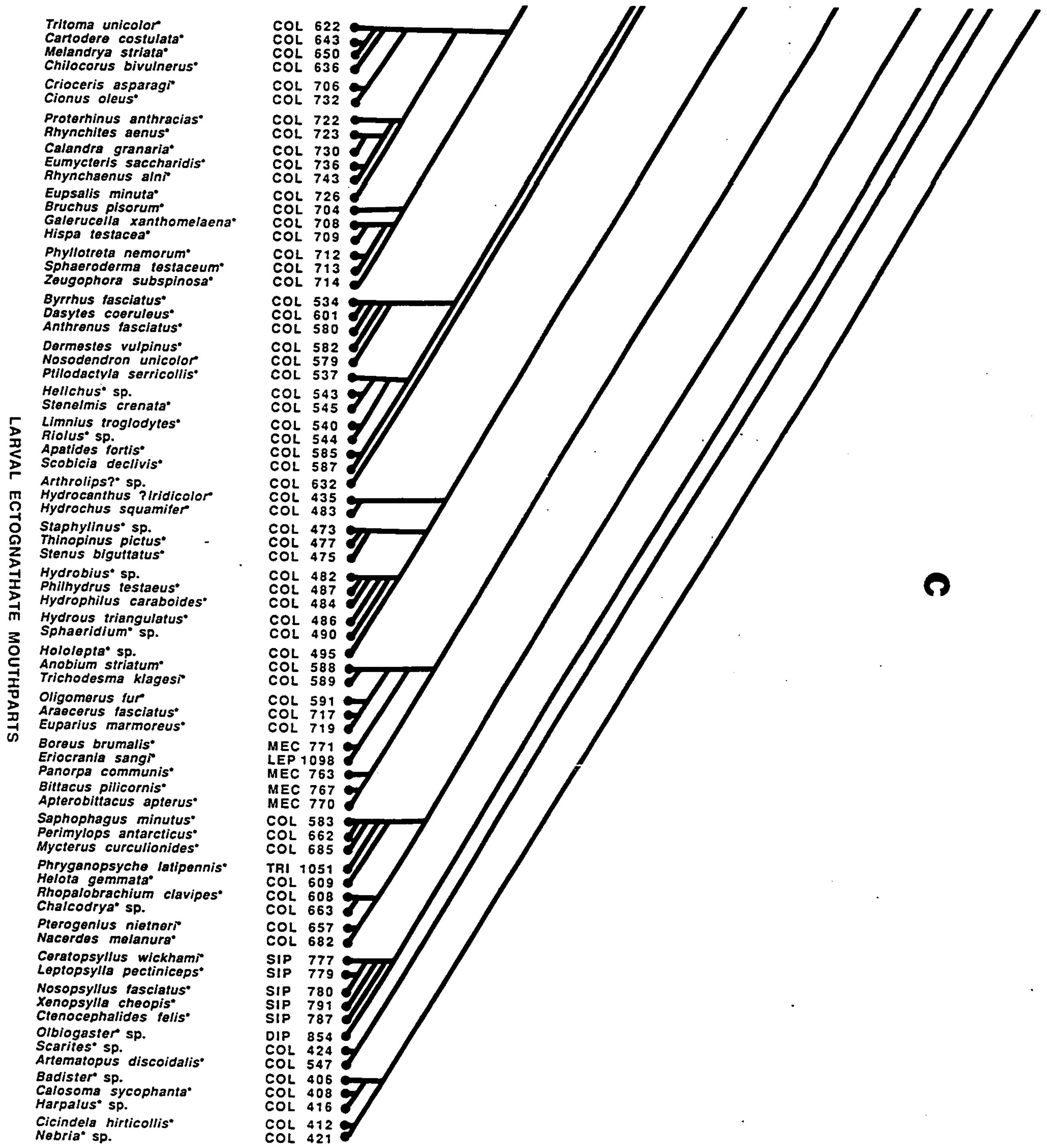

Hydroscapha natans* COL 402
Trichentoma childreni* COL 686
Agriotes* sp. COL 548
Parallelostethus attenuatus* COL 553
Oestodes tenuicollis* COL 556
Alaus oculatus* COL 550
Cebrio antenuatus* COL 555
Horistonotus uhlerii* COL 551
Carabus* sp. COL 410
Loricera* sp. COL 418
Silpha noveboracensis* COL 457
Thanatophilus* sp. COL 458
Sphercheus emarginatus* COL 488
Elodes marginata* COL 501
Prionocyphon discoideus* COL 502
Eucinetus morio* COL 497
Brychius* sp. COL 429
Haliplus* sp. COL 430
Peltodytes* sp. COL 432
Speophyes lucidulus* COL 451
Scydmaenus tarsatus* COL 454
Ochlebius impressus* COL 447
Trichentoma childreni* COL 505
Dascillus cervinus* COL 504
Geotrupes splendidus* COL 516
Passalus cornutus* COL 512
Trox scaber* COL 514
Popilius disjunctus* COL 513
Amphimallon majalis* COL 519
Anastrategus splendens* COL 520
Aserica castanea* COL 521
Melolontha hippocastani* COL 523
Oryctes nasicornis* COL 527
Phyllophaga rugosa* COL 528
Popillia japonica* COL 531
Anisotoma blanchardi* COL 449
Lucanus cervus* COL 508
Sinodendron cylindricum* COL 510
Discoloma cassideum* COL 634
Micropteryx calthella* LEP 1091
Sabatinca barbarica* LEP 1095
a

LARVAL ECTOGNATHATE MOUTHPARTS


Trichonyx sulcicollis* COL 479
Microweisea misella* COL 639
Epicauta pennsylvanica* COL 676
Zonitis bilineata* COL 680
Callityx scabra* COL 593
Tenebroides nanus* COL 595
Enoclarus lecontei* COL 598
Promanus* sp. COL 594
Scotobates calcaratus* COL 671
Alobates pennsylvanica* COL 665
Calopus angustus* COL 681
Holocephala ferruginea* COL 667
Aegialites debilis* COL 691
Hymenorus pilosus* COL 668
Tenebrio* sp. COL 673
Temnochila viriscens* COL 596
Callimeris arcufer* COL 597
Hyporhagus texanus* COL 660
Merinus laevis* COL 669
Synchroa punctata* COL 684
Necrobia rufipes* COL 599
Prostomis mandibularis* COL 683
Scraptia sericea* COL 694
Glischrochilus obtusatus* COL 604
Prometobia sexmaculata* COL 605
Cucujus clavipes* COL 611
Telephanus ?pallidus* COL 613
Pytho niger* COL 688
Neopyrochroa femoralis* COL 689
Anthicus* sp. COL 692
Endomychus coccineus* COL 640
Byturus tomentosus* COL 645
Cis boleti* COL 649
Mycetaea hirta* COL 642
Mycetophagus punctatus* COL 647
Synchita fuliginosa* COL 659
Aulonium tuberculatum* COL 658
Phellopsis obcordata* COL 661
Othnius umbrosus* COL 690
Oryzaephilus surinamensis* COL 612
Antherophagus ochraceus* COL 615
Cryptophagus saginatus* COL 616
Languria angustata* COL 620
Lycoperdina succinata* COL 641
Propalticus simplex* COL 617
Hesperobaenus* sp. COL 644
Orthosoma* sp. COL 700
Rhagium* sp. COL 701

LARVAL ECTOGNATHATE MOUTHPARTS

b


C
LARVAL ECTOGNATHATE MOUTHPARTS
Tritoma unicolor* COL 622
Cartodere costulata* COL 643
Melandrya striata* COL 650
Chilocorus bivulnerus* COL 636
Crioceris asparagi* COL 706
Cionus oleus* COL 732
Proterhinus anthracias* COL 722
Rhynchites aenus* COL 723
Calandra granaria* COL 730
Eumycteris saccharidis* COL 736
Rhynchaenus alni* COL 743
Eupsalis minuta* COL 726
Bruchus pisorum* COL 704
Galerucella xanthomelaena* COL 708
Hispa testacea* COL 709
Phyllotreta nemorum* COL 712
Sphaeroderma testaceum* COL 713
Zeugophora subspinosa* COL 714
Byrrhus fasciatus* COL 534
Dasytes coeruleus* COL 601
Anthrenus fasciatus* COL 580
Dermestes vulpinus* COL 582
Nosodendron unicolor* COL 579
Ptilodactyla serricollis* COL 537
Helichus* sp. COL 543
Stenelmis crenata* COL 545
Limnius troglodytes* COL 540
Riolus* sp. COL 544
Apatides fortis* COL 585
Scobicia declivis* COL 587
Arthrolips?* sp. COL 632
Hydrocanthus ?iridicolor* COL 435
Hydrochus squamifer* COL 483
Staphylinus* sp. COL 473
Thinopinus pictus* COL 477
Stenus biguttatus* COL 475
Hydrobius* sp. COL 482
Philhydrus testaeus* COL 487
Hydrophilus caraboides* COL 484
Hydrous triangulatus* COL 486
Sphaeridium* sp. COL 490
Hololepta* sp. COL 495
Anobium striatum* COL 588
Trichodesma klagesi* COL 589
Oligomerus fur* COL 591
Araecerus fasciatus* COL 717
Euparius marmoreus* COL 719
Boreus brumalis* MEC 771
Eriocrania sangi* LEP 1098
Panorpa communis* MEC 763
Bittacus pilicornis* MEC 767
Apterobittacus apterus* MEC 770
Saphophagus minutus* COL 583
Perimylops antarcticus* COL 662
Mycterus curculionides* COL 685
Phryganopsyche latipennis* TRI 1051
Helota gemmata* COL 609
Rhopalobrachium clavipes* COL 608
Chalcodrya* sp. COL 663
Pterogenius nietneri* COL 657
Nacerdes melanura* COL 682
Ceratopsyllus wickhami* SIP 777
Leptopsylla pectiniceps* SIP 779
Nosopsyllus fasciatus* SIP 780
Xenopsylla cheopis* SIP 791
Ctenocephalides felis* SIP 787
Olbiogaster* sp. DIP 854
Scarites* sp. COL 424
Artematopus discoidalis* COL 547
Badister* sp. COL 406
Calosoma sycophanta* COL 408
Harpalus* sp. COL 416
Cicindela hirticollis* COL 412
Nebria* sp. COL 421

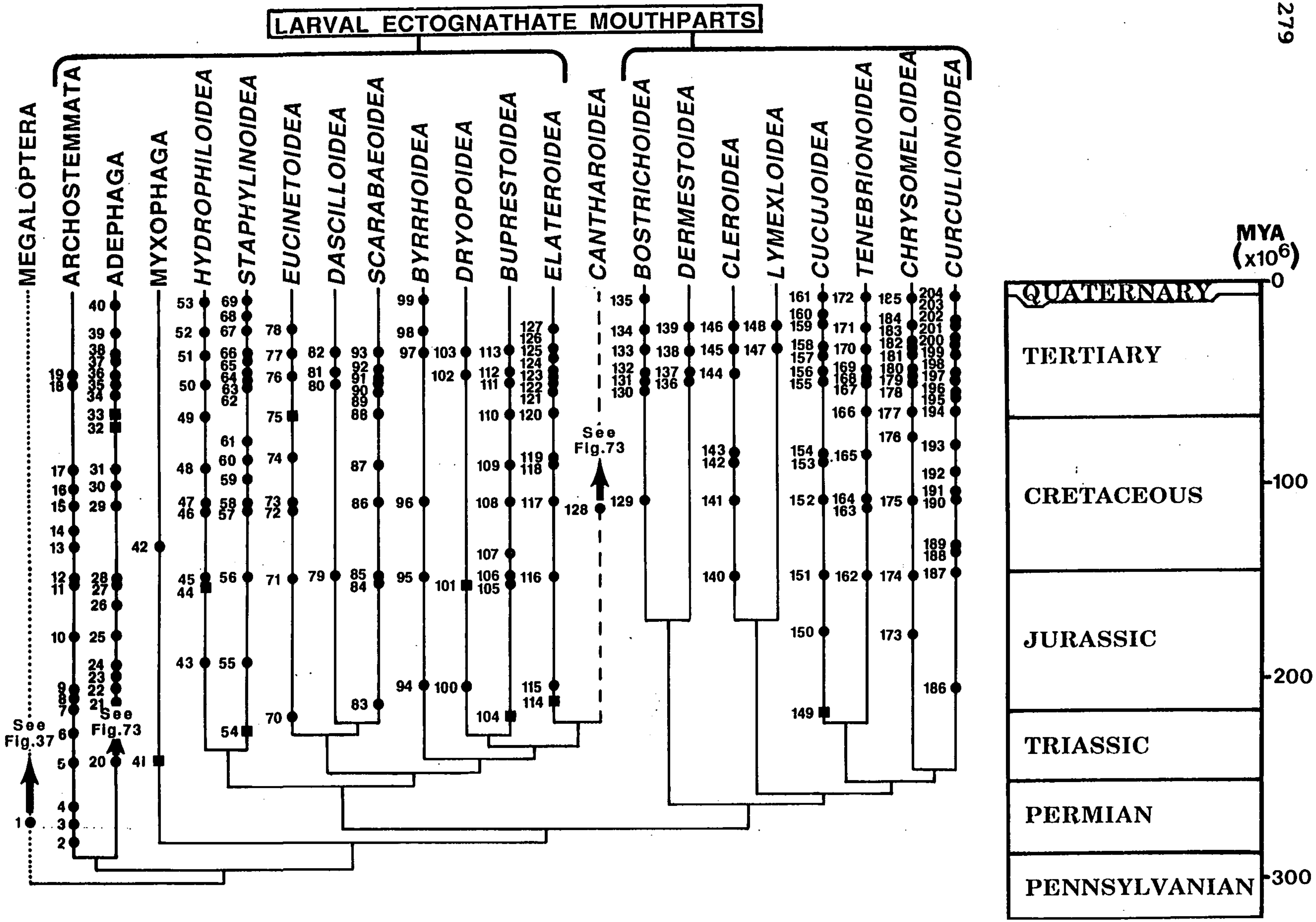
families of adephagan and polyphagan coleopterans and micropterygid lepidopterans. Within this subcluster adephagans and staphylinoid polyphagans are predaceous on other insects whereas the more apomorphic groups--hydrophiloids, eucinetoids, dascilloids, scarabaeoids and cucujoids--are overwhelmingly associated with diets involving the consumption of decomposing wood or litter, roots, fungi and live plant tissue. The micropterygids *Micropteryx calthella* (1091) and *Sabatinca barbarica* (1095) are browsers on mosses and grass stems. Subcluster 3 (479 to 680) comprises predatory pselaphid, coccinellid and meloid coleopterans. The most taxonomically diverse assemblage is Subcluster 4 (593 to 701) and consists of 44 taxa of plesiomorphic coleopterans (Cleroidea, Cucujoidea, Tenebrionoidea, Chrysomeloidea) occurring in a diversity of plant-associated habitats and includes forms that feed on decomposing wood and litter, fungivores and a subgroup of predatory carnivores. Subcluster 5 (622 to 714) is comprised of 10 families of highly plesiomorphic poly phagans (Cucujoidea, Chrysomeloidea, Curculionoidea) that feed on foliage, fungi and to a lesser extent other insects. Members of this subcluster bear well-developed mouthparts for shearing leafy material or macerating fungal sporocarps and mycelia. Subcluster 6 (534 to 587) consists of nine families of coleopterans of an intermediate level of phylogenetic development (Byrrhoidea, Dryopoidea, Dermestoidea, Bostrichoidea, Cleroidea) that occur in live and dead wood, litter, carrion and less commonly on roots and leaves. By contrast Subcluster 7 consists only of the distinctive corylophid *Arthrolips* (Cucujoidea, 632) and is apparently associated with decomposed wood. Subcluster 8 (435 to 495) contains an ecologically different group of predaceous, aquatic or terrestrial coleopterans, namely noterids, staphylinids, hydrophilids and histerids. Subcluster 9 (580 to 770) incorporates wood-boring and litter-consuming bostrichoid and curculionoid coleopterans, four families of carrion-consuming mecopterans and leaf-mining eriocraniid lepidopterans. This ordinally diverse assemblage represents a primary or secondary generalized mouthpart condition, admitting of a rather eclectic spectrum of foodstuffs. Subcluster 10 (583 to 682) includes eight families of dermestoid, cucujoid and tenetrionoid polyphagans and a phryganopsychid trichopteran. These taxa have life-habits that are poorly known, although most forms are apparently associated with wood and others are fungal and sap feeders. Inclusion of an aquatic trichopteran larva in this subcluster is anomalous. Subcluster 11 (777 to 854) comprises maggotlike siphonapteran larvae and one member of the dipteran bibionoid family Anisopodidae. The dipteran larva is structurally similar to the siphonapteran larvae and both have generalized mouthparts. Although siphonapteran larvae are ectoparasitic on warm-blooded hosts, they feed on fur-contained organic debris and sloughed dermal material, and in many respects possess diets similar to the detritivory of larval anisopodids. Subcluster 12 consists of two predatory species, a carabid and an artematopodid. Subcluster 13 (406 to 421) is comprised of entirely predatory carabid species with pronounced mouthpart elements, especially mandibles, for securing prey.

Geochronologic History. A pair of apparently ectognathous jaws, *Rhyniognatha hirsti* Tillyard, were described from the Early Devonian

Rhynie biota of Scotland [104] and were considered larval mandibles by Hirst and Maulik (1926). They are reminiscent of larval coleopteran mandibles. Although Tillyard (1928) considered these mandibles as orthopteroid in origin, recently Whalley (*in* Selden 1985) indicated that *Rhyniognatha* may be a myriapod. Since the taxonomic status of *Rhyniognatha* remains in doubt, the possibility of larval-ectognathates during the Early Devonian can not be excluded (see Kühne and Schlüter 1985).

Recently a caterpillar-like larva exhibiting similarities to the Mecoptera and Hymenoptera was discovered in the Late Carboniferous Mazon Creek locality of the central U.S. [96] (Kukalová-Peck 1988). This earliest documented occurrence of a holometabolous insect confirms the predictions of some (e.g. Malyshev 1968, Köningsmann 1976) that the most plesiomorphic holometabolous insect should be a member of the stem-group of Hymenoptera + Mecoptera, and that its immature stage should be a detritivorous or spore-consuming, ambulatory, eruciform larva similar to a caterpillar. Indirect evidence for Late Carboniferous sporivory and detritivory is present (Labandeira and Beall 1990) although the responsible insects remain unknown. This fossil marks the earliest known occurrence of the larval-ectognathate mouthpart class.

The earliest adult insect fossils whose larvae are members are larval-ectognathates include archostemmatan coleopterans of the family Tschekardocoleidae from latest Carboniferous to earliest Permian deposits from Czechoslovakia (Crowson et al. 1967, but see Kukalová 1969) (Fig. 40). Undoubted archostemmatan coleopterans occur in younger Early Permian strata of the Kuznetsk Basin from the USSR [97]


LARVAL ECTOGNATHATE MOUTHPARTS
MEGALOPTERA
ARCHOSTEMMATA
ADEPHAGA
MYXOPHAGA
HYDROPHILOIDEA
STAPHYLINOIDEA
EUCINETOIDEA
DASCILLOIDEA
SCARABAEOIDEA
BYRRHOIDEA
DRYOPOIDEA
BUPRESTOIDEA
ELATEROIDEA
CANTHAROIDEA
BOSTRICHOIDEA
DERMESTOIDEA
CLEROIDEA
LYMEXLOIDEA
CUCUJOIDEA
TENEBRIONOIDEA
CHRYSOMELOIDEA
CURCULIONOIDEA
See Fig.37
See Fig.73
See Fig.73
MYA (x10^6)
0
100
200
300
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
PENNSYLVANIAN

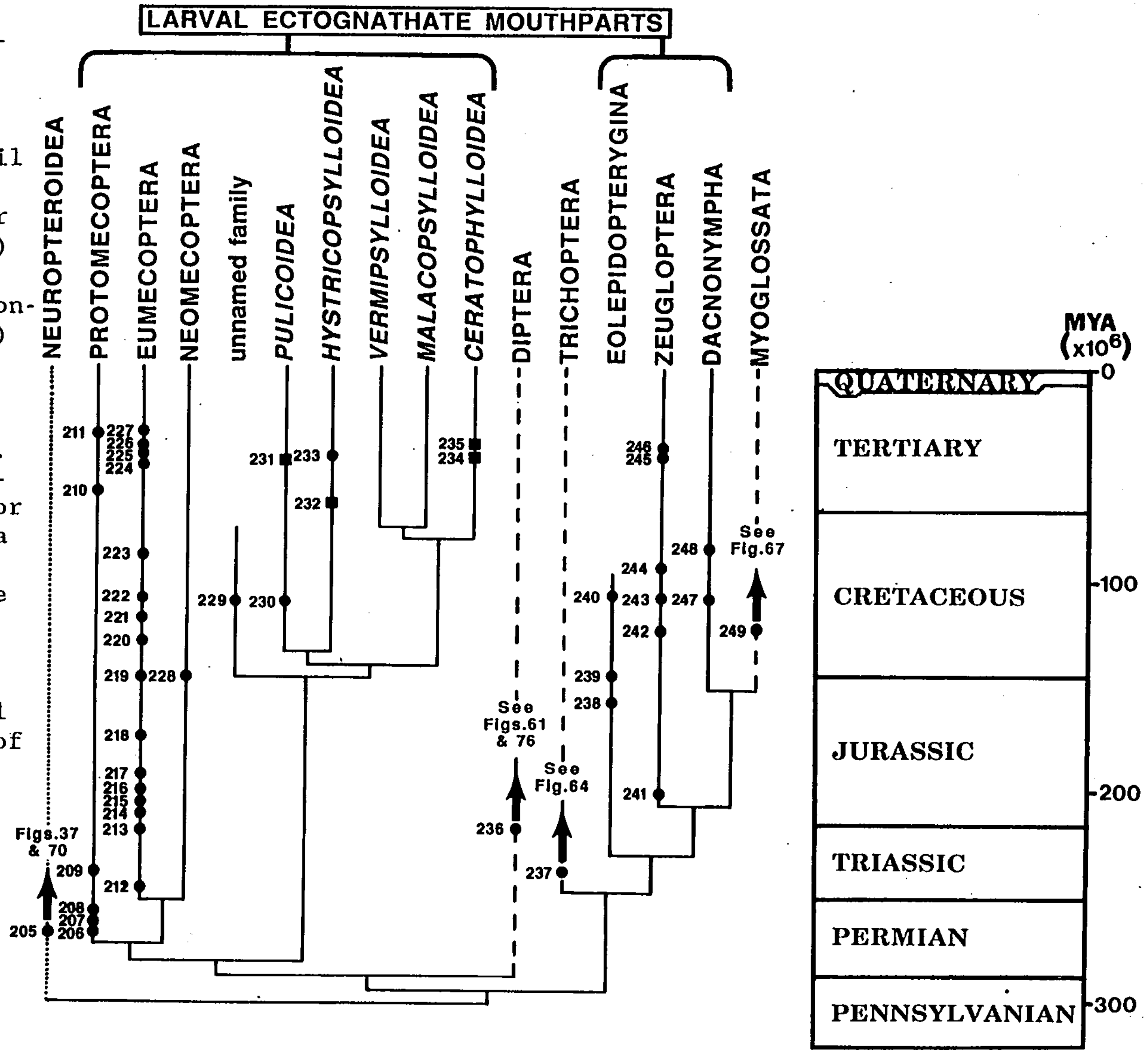


FIGURE 40. Geochronologic history of the Larval Ectognathate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Crowson (1981) for Coleoptera, Willmann (1987) for Mecoptera, Traub and Rothschild (1983) for Siphonaptera, and Razowski (1974) and Kristensen (1984) for Lepidoptera; interordinal relationships after Hennig (1981) and Jamieson (1987). The taxonomic level of analysis is the superfamily for Coleoptera and Siphonaptera and the suborder for Mecoptera and Lepidoptera. The outgroups are Megaloptera and Neuropteroidea. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.

(Rohdendorf et al. 1961, Ponomarenko 1969). The earliest occurring fossil adephagans are several taxa from the Early Triassic of the USSR [82] (Ponomarenko 1977b) and the earliest record of polyphagans is probably a silphid from the Late Triassic of South Africa [78] (Ponomarenko 1977b), although slightly younger probable nitidulids and buprestids have been recorded from the eastern U.S. [76] (Olsen et al. 1978). The earliest reliable occurrence of a polyphagan are ademosynids from the Late Triassic of the USSR (Ponomarenko 1977b; Crowson 1981).

The earliest adult mecopteran body fossils are wings found in the Late Carboniferous to Early Permian deposits of the Kusnetsk Basin [97] (Martynova 1958, Rohdendorf et al. 1961). Numerous mecopteran taxa have been described from this locality, including the archaic family Protomeropeidae. Somewhat younger taxa are recorded from the Early Permian deposits from Elmo, Kansas (90] (Tillyard 1926b) and Chekarda, USSR [89] (Zalessky 1946). The earliest documented eumecopterans are nannochoristids and robinjohnids from the Late Permian of New South Wales, Australia [83] (Tillyard 1926d, Riek 1970b). Neomecopterans consist of the single family Boreidae and have a poor fossil record; the only confidently assigned occurence is from the Middle Jurassic of the USSR (Rasnitsyn 1988). As is typical for parasitic insects, siphonapterans have a very poor fossil record. Pulicoids and an unnamed family has been documented from the Lower Cretaceous of Victoria, Australia [53] (Jell and Duncan 1986), although younger, Baltic amber [19] specimens have been known for a long time (Dampf 1910). It is possible that siphonapterans extend to the Late Paleozoic since there is convincing evidence for a sister-group relationship with the Mecoptera (Jamieson 1987, Willman 1989). It is highly likely that the anisopodid dipteran, a member of the larval ectognathate mouthpart class (no. 854) and a member of the superfamily Bibionoidea, had ancestors during the Late Triassic since bibionid nematocerans have been recorded from Eastern US sediments of this age [76] (Olsen et al. 1978). Since zeuglopteran micropterygids and dacnonymphan eriocraniids are also larval-ectognathates, their fossil history can be traced respectively to the Early Jurassic of England [69] (Whalley 1985) and to the Early Cretaceous of the USSR [52] (Skalski 1979a, Whalley 1986).

The body fossil record of the adult stages of larval ectognathates currently indicates an origin during the Late Carboniferous and gradual, restrained expansion during the Permian, followed by an adaptive radiation of particularly coleopterans during the Triassic (Fig. 40). By the Late Jurassic there is fossil evidence for the existence of 17 of the 20 major suborders and polyphagan superfamilies. Mecopterans probably experienced a similar initial rise in numbers, although their family-level Permian diversity was twice their extant diversity (Carpenter and Burnham 1985). Circumstantial evidence from a diverse Upper Triassic fauna of dipterans [73] (Rohdendorf 1974, 1980) and the occurrence of Mecoptera as the sister-group to Diptera during the Late Carboniferous and Early Permian indicates that plesiomorphic dipterans probably experienced at least a modest taxonomic expansion during the Permian and Triassic.

Much of the success of insects has been attributed to the decoupling of a immature, nutritive phase from an adult, reproductive phase, such that a species could conveniently exploit two different environments that are temporally displaced for providing year-round sustenance (Hinton 1977). The direct fossil documentation of this transition from a nonmetamorphic- to a metamorphic-dominated fauna is difficult since larvae are invariably soft-bodied and do not preserve as well as their more sclerotized adults. However, during the Late Carboniferous, the nonmetamorphic component of the insect fauna was probably close to 95% judging from the rarity of fossils morphologically assignable to metamorphic clades; currently metamorphic insects constitute 88% of the total insect fauna (Appendix D). Adult fossil evidence indicates this major developmental shift occurred during the Permian and by the Early Triassic the insect fauna was essentially modern (Sepkoski and Hulver 1985). Thus during the Early Mesozoic or earlier, larval instars must have invaded myriad habitats and established themselves as major ecosystem elements. (The fossil documentation of other larval mouthpart classes during the Late Paleozoic and Mesozoic is provided by sections dealing with the geochronologic histories of the mouthbrush, mandibulobrustiate, sericterate, fossate-complex, tubulomandibulate and mouthhook mouthpart classes.)

Evidence for the presence and diversification of larval-ectognathates can be inferred from the relatively rich fossil record of their respective adult stages. This approach allows for the extrapolation of many larval life-habits into the Mesozoic, with times of origination determined by cladogenetic relationships and fossil occurrences of relevant sister-groups. Given the phylogram of Fig. 40, most major larva life-habits, including aquatic and terrestrial predators, external foliage feeders, wood-borers, carrion-feeders, fungivores and others can be extended to the Early Jurassic for most superfamilies. Alternative approaches consider (i) the indirect evidence of trace fossils, particularly insect damage on seed plants and (ii) the limited fossil record of relevant larvae.

With the probable exception of leaf-mining (see Section 8.3.14), wood-boring has the second best fossil record for indicating insect damage on vascular plants. Except for wood-boring from Late Carboniferous swamp forests (Cichan and Taylor 1982, Scott and Taylor 1983, Labandeira and Beall 1990), the earliest known documentation of coleopteran-mediated wood-boring originates from Late Triassic petrified woods of the Chinle Formation of Arizona [77] (Walker 1938) and the Keuper Series of Germany (Linck 1949). Walker (1939) attributed three distinctive patterns of subcortical tunnels to buprested and curculionid adults and larvae, whereas Linck (1949) considered his penecontemporaneous borings to be constructed by larval anobiid beetles. Crowson (1981) has interpreted both occurrences as evidence for wood-boring by larval archostemmatans such as ommatids and cupedids. From a Middle Jurassic deposit of China, Zhiyan and Bole have described from a permineralized gymnosperm a fecal pellet-laden burrow networks with reaction tissue. Although they attribute their burrow galleries to adult coleopterans, a larval coleopteran culprit is more likely. From the Early Cretaceous of England (57] Blair (1943) described scolytinetype subcortical burrows on a probable conifer, although Crowson (1981) prefers a nonscolytine curculionid with scolytine-habits as the culprit. Finally Delevoryas (1968) has presented good evidence for insect-mediated tissue damage to the strobilar axes of Early Cretaceous cycadeoids [50]. Crowson (1981) interprets this cycadeoid damage as originating from phalacrid or byturrid larvae and is similar in style to the damage these larvae make on capitula of extant Compositae.

The fossil record of larval-ectognathates is biased toward preservation of freshwater forms. Ponomarenko (1977b) has described predatory aquatic larvae of the extinct dytiscid-like Parahygrobiidae from the Middle/Late Jurassic of the USSR [62]. Larval parahydrobiids bore conspicuous, falcate mandibles and relatively long, maxillary palps. From the Late Jurassic Karatau deposits of the USSR [60] Ponomarenko (1977b) has also figured a probable helophorine scarabaeid larva (Crowson 1981) that inhabited a freshwater or possibly brackish environment. A first instar larva of the archostemmatan *Micromalthus* has been noted from Lebanese amber [55] by Crowson (1981). The large, predaceous aquatic larvae of the extinct Coptoclavidae was found from the Lower Cretaceous of Mongolia and has been restored by Ponomarenko (1977b). Lastly, Jell and Duncan (1986) have identified several predaceous, aquatic and terrestrial larvae from the Lower Cretaceous of Victoria, Australia [53]. Described forms include dytiscids, hydrophilids, helodids and a mecopteran belonging to *Nannochorista*.

These data collectively document some of the habitats occupied by larval-ectognathates during the Mesozoic. Because of the poor preservational potential of larval ectognathates, much of their historical expansion onto terrestrial and freshwater habitats can currently only be inferred from the fossil records of their respective adult stages.

Previous Designations. When compared to discussions of other mouthpart types, the distinctive larval mouthparts of mecopterans, siphonapterans, generalized nematoceran dipterans, primitive lepidopterans and especially most coleopterans, have been ignored. Apparently the masticatory mouthparts from larvae of mandibulate coleopterans and many other holometabolous groups have been considered versions of their respective adult chewing mouthparts. Thus the intrinsic distinctiveness of larval mouthparts (Fig. 28) has been subsumed under a broader category of "chewing mouthparts" in most reviews of the subject.

The earliest recorded mention of insect mouthparts that could include larval-ectognathates was Aristotle, who mentioned insects "having teeth and being omnivorous" in his *De Partibus Animalium* (Morge 1973). During the Modern Era Fabricius (1775, 1799) provided keys for mandibulate insects, although holometabolous larvae were never discussed. Subsequently MacLeay (1921) and Latreille (1832) considered coleopteran larvae as "mandibulate." About a century later Metcalf (1929) was one of the first to include holometabolous larvae in his class of "Chewing Type" mouthparts within his Mandibulate Series. This inclusion was followed by Metcalf et al. (1962), but was not adopted in James and Harwood's (1969) textbook on medical entomology. Mouthparts of relevant holometabolous larvae was minimally discussed in Matsuda's

(1965) review and was not mentioned by Smith (1985) or Chaudonneret's (1982-1989) extensive synthesis (see Table 6 for further details).

Bitsch (1966) presented the first general, comprehensive treatment of larval coleopteran mouthparts. He grouped all larval coleopteran mouthparts into three categories, based on a primitive to derived series. The principal evolutionary trends involved incorporation of the clypeus and labrum into the cranium, reduction of the posterodorsal regions of the cranium and expansion of the posteroventral region. Denis and Bitsch (1973) recapitulated much of Bitsch's earlier work on coleopterans and also provided good descriptions of mecopteran, siphonapteran and micropterygid lepidopteran mouthparts, without considering them a unified mouthpart grouping. Crowson (1981) devoted several pages in describing the *Bauplän* of the larval coleopteran head capsule and mouthparts. Crowson's presentation is the best summary of what is herein designated as the **larval-ectognathate** mouthpart class. Although Crowson made no mention of mecopteran, siphonapteran, primitive nematocan and micropterygid heads and mouthparts in his review of coleopteran biology (1981), the phenetic similarities in structure of these groups are sufficiently strong (Fig. 39) that his account is a good approximation for the entire mouthpart class. To my knowledge, the term, larval-ectognathate, has no precedent of usage in the entomological literature.

Review of Literature. Since coleopterans constitute overwhelmingly the bulk of diversity in the larval ectognathate mouthpart class, coleopteran data-set sources will be discussed first. Primary data sources for the 149 coleopterans of the larval-ectognathate mouthpart class were Böving and Craighead (1931) and Peterson (1951) which were essential for comprehensive descriptions of head and mouthpart structure for 114 of these taxa. Accompanying these two invaluable reference works were secondary sources that treated particular mouthpart regions or taxonomic groups. Studies of head and mouthpart regions of selected larval coleopterans include Crampton (1921c) for several representative taxa, Anderson (1936) for the larval labium, Das (1938) for general mouthpart structure and musculature, Dorsey (1943) for structure and musculature of the labrum, labium and pharynx and DuPorte (1946) for comparisons of archetypes of larval cephalic capsules. Taxonomically-based treatments include Verhoeff (1923) for Tenebrionoidea, Howden (1955) for Geotrupidae, Grandi (1959) for Chrysomelidae and Striganova (1967) for head and mandible structure of various larvae burrowing or boring into indurated substrates.

In addition to the two primary sources and the above ancillary reference works, other general sources were available for providing confirmatory or missing data. These include Merritt and Cummins (1984) and McCafferty and Provoshna (1984) for aquatic larvae, and Snodgrass (1928, 1935, 1960), Arnett (1963), Richards and Davies (1977) and Crowson (1981) for terrestrial and aquatic forms. These latter sources also provided valuable dietary data.

Head and mouthpart structures for approximaely 35 of the coleopteran larval taxa were provided by isolated sources. Most of these sources are complete descriptions for particular species. For the Adephaga the carabid taxa *Badister* sp. was described by Ghilarov (1964), *Loricera* sp. by Bauer and Kredler (1988) and *Nebria* sp. by Evans (1965b, 1965c) and Forsythe (1982). Mouthpart and head structures of the haliplid taxa *Brychius*, *Haliplus* and *Peltodytes* were described by Jaboulet (1960). Among the Polyphaga the mouthpart structure of several staphylinid taxa were studied, including the leiodid *Speophyes lucidulus* (Delarouzee) by Feiffe (1965) and Corbière (1967), the scymaendid *Scymaenus tarsatus* Müller by Meinert (1988), the aberrant staphylinid *Stenus biguttatus* Linneaus by Weinreich (1968), and the pselaphid *Trichonyx sulcicollis* Reichenbach by Besuchet (1956). Moulins (1959) examined the head and mouthpart structures of several hydrophilids, including *Hydrobius* sp., *Philhydrus testaceus* Fabricius and *Hydrophilus caraboides* Linneaus; Quennedey (1965) similarly described *Sphaeridium*.

Descriptions of head and mouthparts from taxa of Eucinetoidea include the eucinetid *Eucinetus morio* LeConte by Lawrence and Newton (1980) and the scirtid *Elodes marginata* Fabricius by Carpenter and MacDowell (1912), Beier (1952) and Matsuda (1965). The dascilloid *Dascillus cervinus* Linneaus was examined by Carpenter and MacDowell (1912). Among the Scarabaeoidea the passalid *Popilius disjunctus* Illiger was treated by Hiznay and Krause (1955) and the scarabaeids *Amphimallon majalis* (Razoymonski) by Butt (1944), *Melolontha hippocastani* Fabricius by Subklew (1938) and *Oryctes nasicornis* Linneaus by Crome (1957). For the Drypoidea the limnichid *Limnius volkmari* Panzer was described by Delachambre (1965) and the dryopid *Riolus* by Marvillet (1960). The elateroid *Artematopus discoidalis* Pic, an artematopid, was examined by Costa, Cassari-Chen and Vanin (1985). Head and mouthpart studies of dermestoids include the dermestids *Anthrenus fasciatus* Herbst by Pradhan (1950), *Dermestes vulpinus* Fabricius by Robin-son (1930) and the anobiid *Anobium striatum* Linneaus by Verhoeff (1923).

Many studies have detailed head and mouthpart structure for the apomorphic superfamilies Cucujoidea, Tenebrionoidea, Chrysomeloidea and Curculionoidea. For the Cucujoidea, the phloestichid *Rhophalobrachium clavipes* Bohemann and the propalticid *Propalticus simplex* Crowson and Sen Gupta were described by Sen Gupta and Crowson (1966), the languriid *Languria angustata* Beauvois by Baker and Ellsbury (1988), the erotylid *Tritoma unicolor* Say by Rymer-Roberts (1958), the discolomid *Discoloma cassideum* Reutter by Emden (1932), and the coccinellid *Microweisea misella* LeConte by Gage (1920). For tenebrionoids, several have been examined, namely the pterogeniid *Pterogenius nietneri* Candeze by Lawrence (1977), the perimylopid *Perimylops obcordata* Kirby by St. George (1939) and Watt (1970), the oedomerid *Nacerdes melanura* (Linneaus) by Rozen (1958), the mycterid *Mycterus curculionoides* Fabricius by Crowson and de Viedma (1964), and the trichentomid *Trichentoma childreni* Gray by Gahan (1908). The chrysomelid *Hispa testacea* Linneaus was figured by Grandi (1959) and the curculionid *Eumycteris sacchardis* Barber by Böving (1927a).

Larval mecopterans are minimally documented; only four taxa with complete documentation could be located. The panorpid *Panorpa communis* Linneaus was described by Crampton (1917b, 1921c), Das (1938), Bierbrodt (1943) and Snodgrass (1947), the bittacid *Bittacus pilicornis* Westwood by Setty (1940) and Peterson (1951), the apterobittacid *Apterobittacus apterus* (MacLachlan) by Applegarth (1939), Cook (1944) and Snodgrass (1947), and the boreid *Boreus nivoriundus* Fitch by Peterson (1951).

Larval siphonapterans do not fare much better, with only five taxa having complete descriptions, all which are ceratophyllids and pulicids. For the Ceratophyllidae Sikes (1930) and Johnson (1957) described *Ceratophyllus wickhami* Baker and an allied species, Perfiljew (1927) examined *Leptopsylla pectiniceps* Wagner, and Sharif (1937) and Elbel (1951) documented *Nosopsyllus fasciatus* (Bosc). The pulicids *Ctenocephalides felis* (Bouché) was described by Peterson (1951) and Elbel (1951) and *Xenopsylla cheopis* Rothschild by Sikes (1930). The nematoceran anisopodid *Olbiogaster* sp. was described by Anthon (1943b).

Current interest in the phylogeny of primitive lepidopterans (e.g. Kristensen 1968a to 1984b) has resulted in the documentation of head and mouthpart structure and ecology of many small, rare, plesiomorphic moths. Relevant taxa for the larval ectognathate mouthpart class include the micropterygids *Micropteryx calthella* Linneaus, documented by Busck and Böving (1914), Portier (1949) and Lorenz (1961), and *Sabatinca barbarica* Philpott, documented by Tillyard (1922) and Snodgrass (1935). The eriocraniid *Eriocrania sangi* Wood and an allied species were described by Tragardh (1913), Jayewickreme (1940) and Hasenfuss (1969). The phryganopsychid trichopteran *Phryganopsyche latipennis* (Banks) was documented by Wiggins (1959).

8.3.6. Maxillolabiate Class
(Class 5)

Description. Head quadrate; proboscis absent to inconspicuous; gula and genae prominent to moderately developed. Antennae geniculate; ocelli 3 or absent; eyes expansive to moderately-developed. Food pump pharyngeal, with or without a clypeal pump. Mouthparts symmetrical, mandibulate, nonretractile and either hypognathous or prognathous.

Clypeus quadrate to transversely elongate; single or rarely rused to frons. Labrum single or absent; if present, quadrate to vertically elongate, with margin variously developed (pectinate, mucronate or curvilinear). Hypopharynx an inconspicuous lobe; epipharynx setate or absent. Mandibles dicondylic; falcate to less commonly quadrangular; incisiform; musculation of adduction/abduction. Maxillae fused to labium as maxillolabial complex. Maxillary stipes elongate to equant; lacinia penicillate, unmodified or absent; galeae pectinate or lobate. Maxillary palpus of variable segmentation, filiform-clavate or rarely serrate, long to very long. Labium generally complete; glossa rasp-like; paraglossae pectinate or absent. Palps 3- or 4-segmented, long to very long. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. Maxillolabiates are the only mouthpart class to possess an unmodified, nonprotractile laxillolabial complex and are distinguished from the glossate condition (Section 8.7.2) which is characterized by specializations of the maxillolabial complex and other mouthparts for fluid-feeding in deep cavities. Maxillolabiates possess prominent mandibles as the major organs of food procurement rather than the variously descleritized, excavate mandibles of glossates. Incisiform, falcate mandibles, an inconspicuous lobe-like hypopharynx and a scrobinate glossa are stereotypical elements of maxillolabiates. Although maxillolabiates are superficially similar to adult-ectognathates

(Section 8.3.4), adult-ectognathates are less stereotyped as a mouthpart class and lack the characteristic maxillolabiate complex.

Diversity and Natural History. Maxillolabiates constitute an ecologically important mouthpart class that includes approximately 46,600 species of apocritan hymenopterans in 15 families (Appendix D) that occur in virtually all terrestrial habitats except extreme polar or alpine zones. This diversity corresponds to a rank-order of 9 among 34 mouthpart classes (Table 5, Fig. 131), indicating a modest importance in the modern hexapod fauna. The taxonomic membership of maxillolabiates includes families from the superfamilies Proctotrupoidea and Chalcidoidea of the Hymenoptera Parasitica and seven families belonging to the superfamilies Chrysidoidea, Tiphioidea, Vespoidea, Formicoidea and Sphecoidea of the Hymenoptera-Aculeata. Maxillolabiates are parasitoids or parasites on other arthropods, and less commonly free-living, subsocial to eusocial omnivores; as a group they possess a very eclectic dietary spectrum (Fig. 41).

Members from both maxillolabiates and glossates are often present in the same taxonomic family, an occurrence attributable to their joint possession of a maxillolabial complex. However glossates have developed specializations for elongation of maxillolabial elements for reaching into deep cavities for lapping surface fluids whereas maxillolabiates have an abbreviated, unelongated maxillolabial complex used for manipulating solid food sequestered by large, trophic mandibles. Whereas glossates are overwhelmingly nectarivorous, maxillolabiates are insectivorous or less commonly omnivorous. In glossates the female sting is

INCLUDED TAXA:
Hymenoptera (Apocrita)

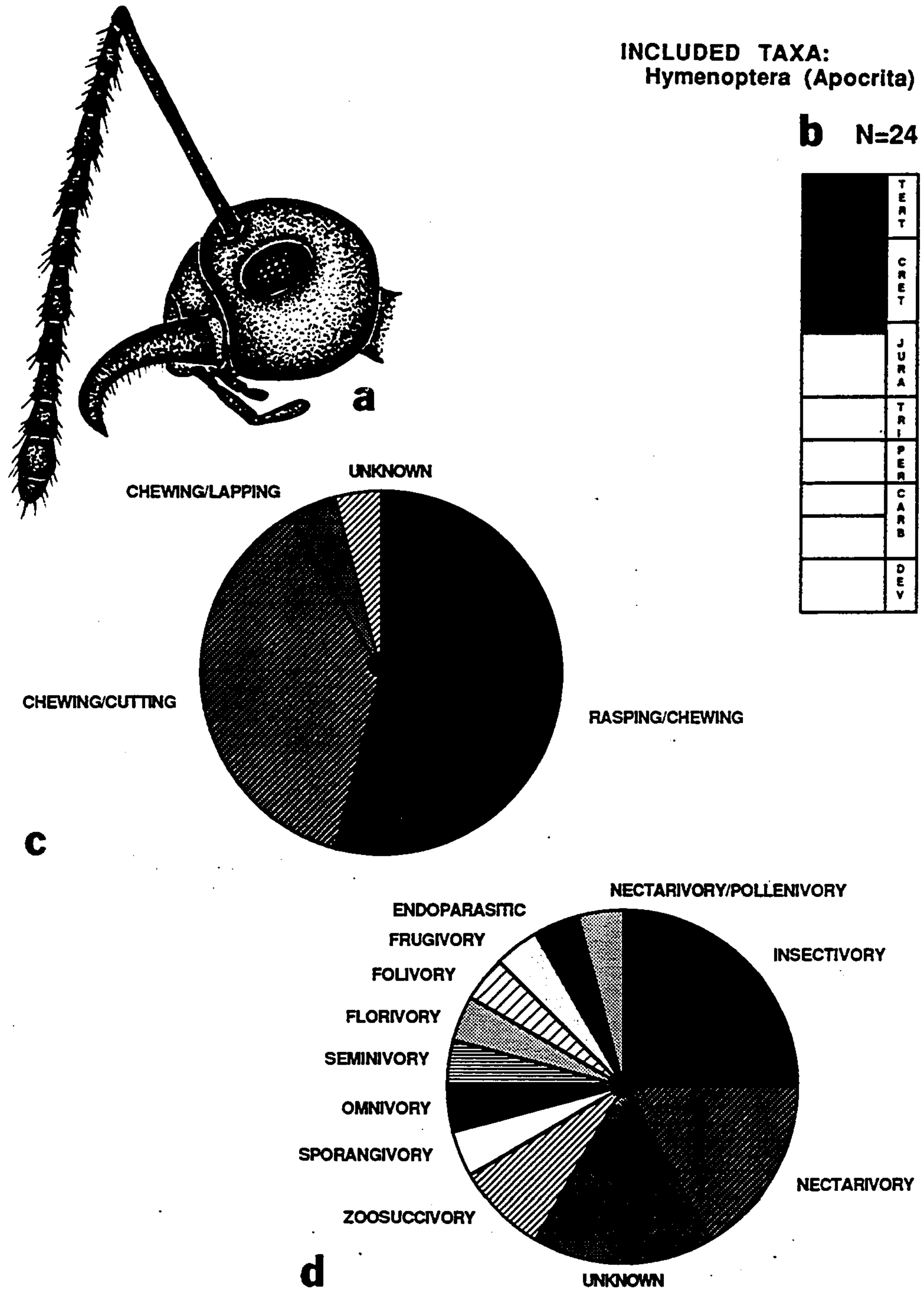


FIGURE 41. Overview of the Maxillolabiate Mouthpart Class. a, *Oecophylla smaragdina* Fabricius (Hymenoptera: Formicidae, data-set no. 1323), after Wheeler (1910); b, taxonomic distribution, numbers of taxa discovered and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

used individually or collectively (in a swarm) for defensive purposes whereas in maxillolabiates the sting is used for paralysis of prey. The prey is used as a substrate for either the oviposition of eggs that will later parasitize the prey, or the prey is transported to a larval domicile where it is immediately consumed.

In the discussion that follows, an emphasis will be placed on one particular group of maxillolabiates, the ants, which comprise about 30% of all maxillolabiates (about 14,000 species). This is because of the relatively intense effort devoted to the study of ants, spurned in part by major monographic accounts of Wheeler (1910), Wilson (1971) and Wilson and Hölldobler (1990).

As a group, maxillolabiates other than ants have a mixed diet that is dominated by insect protein and supplemented by pollen and nectar (Faegri and van der Pijl 1980, Stradling 1987). However the degree to which nectarivory exists in maxillolabiates is interesting since it suggests a life-habit that may be antecedent to the obligate nectarivory of glossates. Among proctotrupoids, the diets of adults are poorly known, although it is likely there is feeding on surface liquids such as nectar, honeydew of surface exudates from parasitized larval hosts (Vinson and Barbosa 1987). Among the Chalcidoidea there is significant adult imbibation of surface plant fluids, although the feeding habits of many species remain unknown because of their very small size. Chalcidids have been implicated in the pollination of *Ficus* (Moraceae) and perilampids feed on flowers, aphid honeydew or leaf exudates (Proctor and Yeo 1973). Chrysidoids are somewhat better known and possess the same feeding habits. Dryinids feed on the honeydew of homopteran nymphs that they parasitize for larval food; on occasion they will imbibe honeydew without injury to the homopteran (Willemstein 1987, Gauld and Bolton 1988). Adult female bethyliids will imbibe haemolymph that oozes from the sting sites of paralized coleopteran or lepidopteran larvae (Gauld and Bolton 1988), a possible behavioral precursor for the imbibation of plant sap or nectar (Willemstein 1987). Scolebythids have unknown feeding habits. Among the tiphioids, bradynobaenids are suspected anthophiles, possibly pollen-collectors, although reliable data is lacking (Willemstein 1987). One nectarivorous species of the related tiphiids are involved in pollination of Australian orchids by pseudocopulation (Armstrong 1979). Vespoids have well-documented feeding habits and are nectarivorous and surface fluid feeders on ripe fruit and honeydew as adults, although they capture insect prey as food for their larvae (Richards and Davies 1977, Armstrong 1979). On occasion they will regurgitate stored fluid food in their crop as nutriment for developing larvae. Sphecoids as a group paralyze a diverse assemblage of insects for larval food and feed on floral and extrafloral nectaries (Gauld and Bolton 1988) but are insignificant as pollinators (Proctor and Yeo 1973).

By comparison to apocritan wasps, the feeding ecology of ants has been extensively documented (Wheeler 1910, Carroll and Janzen 1973, Stradling 1987, Wilson and Holldobler 1990). The conspicuousness of ants in most ecosystems is at least partly attributed to the origin of an wingless worker caste that is able to forage in inaccessible microhabitats far from its nest (Wilson 1971). Unlike termites (to which they are often compared), ants are fundamentally predaceous and are not restricted to sites containing ample supplies of cellulose (Wilson 1971). Finally the presence of a metapleural gland, which secretes substances inhibitory to micro-organismic growth, is important in maintaining domicile sanitation. As a family, formicids (ants) may have the most eclectic diet of any insectan family, with specialist and generalist species hunting mobile insect prey, raiding nests of social insects, collecting seeds, scavenging, harvesting fungal mycelia from cultured plant debris and sequestering homopteran honeydew and nectar (Carroll and Janzen 1973). They are also important detritivores, sarcophages and predators in carrion communities (Braack 1987). Because of this unique dietary spectrum, distinctive foraging style and eusociality, they are considered as a separate feeding guild and comprise a dominant arthropod feeding guild in many ecosystems (Stork 1987).

In addition to a broad dietary reprertoire, ants have established many mutualisms with plants, the most notable is the ant/acacia thorn commensalism (Janzen 1966). In certain *Acacia* species (Fabaceae) of Africa and South and Central America, ants inhabit the enlarged bulbous bases of the stipular thorns. These ants feed on extrafloral nectar, nutritive exudates from Beltian bodies on the pinnule tips, honeydew from tended aphids on the plant and all accidental animals that wander into the tree. In return the ants provide protection to the plant by consuming or otherwise deterring all herbivores attempting to predate on the plant (Hocking 1980). Matthews (1976) has suggested that the acacia/ant mutualism originated evolutionarily from ants that inhabit advanced-stage galls caused by other insects. Another mutualism has been described by Gray et al. (1989) wherein ants inhabit the hollow pseudobulbs of epiphytic orchids in Mexico, packing the central cavities with debris, including dead insects, seeds and sand. Metabolic uptake of these materials by the plant was demonstrated, indicating an advantage to the orchid in the sequestering of nutrients--an advantage that orchid conspecifics without the mutualism would lack. A third mutualism involves seed-collecting ants that are attracted to the oily, lipid-rich elaiasome of *Calathea* (Marantaceae) seeds. After seed fall, several ant species transport and caché these seeds to various habitats, where germination may ensue if they are not readily consumed (Abrahamson 1989).

There is some debate regarding the role of ants as pollinators. Armstrong (1979) described a case of worker ants pollinating an orchid by feeding on nectar secreted by the orchid labellum. Frost (in Proctor and Yeo 1973) cited a case in which rupturewort (Caryophyllaceae), a small, sprawling plant with minute, honey-scented flowers is pollinated by ants. These and a few other cases led Faegri and van der Pijl (1980) to consider ants as important pollinators in hot desert habitats. They predicted that ant pollinated plants should have a clumped distribution and bear flowers that are close to the ground, small, sessile, inconspicuous, and with sweet-scented but minimal nectar rewards. Such plants would select for pollinators that are ambulatory, nonflying insects resistant to elevated soil surface temperatures. It should be noted however that ants have rather smooth, nonhairy body surfaces to which pollen does not adhere and their small size allows them to bypass stamens in larger flowers with deep-seated nectar (Armstrong 1979). However, their extremely high abundance in many ecosystems, including deserts (Wilson 1971), may compensate for this structural deficiency.

Structural Themes. Three discrete subclusters distinguish maxillo-labiate mouthparts (Fig. 42). These are (i) a seeming heterogenous group comprising a bradynobaenid (Tiphioidea), a plumariid (Chalcidoidea) and the only nonhymenopteran in the class, the hydrophilid beetle *Berosus*, (ii) an ant dominated subcluster and (iii) a wasp dominated group of chalcidoids, chrysidoids and a proctotrupid. The inclusion of a beetle in the first group is attributable to the presence of sufficiently similar character-states so as to indicate a high similarity to the two other members of the cluster, even though several key character-states that are important for maxillolabiates are absent between *Berosus* and the two othermembers.

The ant-dominated subcluster comprises a structurally well-unified group. This assemblage contains taxa that bear a falcate mandible, fimbriate galeae, a scrobinate glossa and other features that separate the ant-dominated subcluster from the two others. The wasp-dominated subcluster by contrast has several distinguishing features in almost all of its members, including absence of a labrum, lacinia and paraglossae, and presence of three ocelli instead of the ocellar absence that is typical of ants.

Geochronologic History. Members of the most primitive hymenopteran group, the Xyelidae of the suborder Symphyta, have a fossil record extending to the Early Triassic of the USSR [82] (Rasnitsyn 1969). The derived group, suborder Aprocrita, is characterized by a pedunculate waist and a piercing/stinging rather than a sawing/boring ovipositor; it originated sometime during the Early Jurassic (Rasnitsyn 1980), as

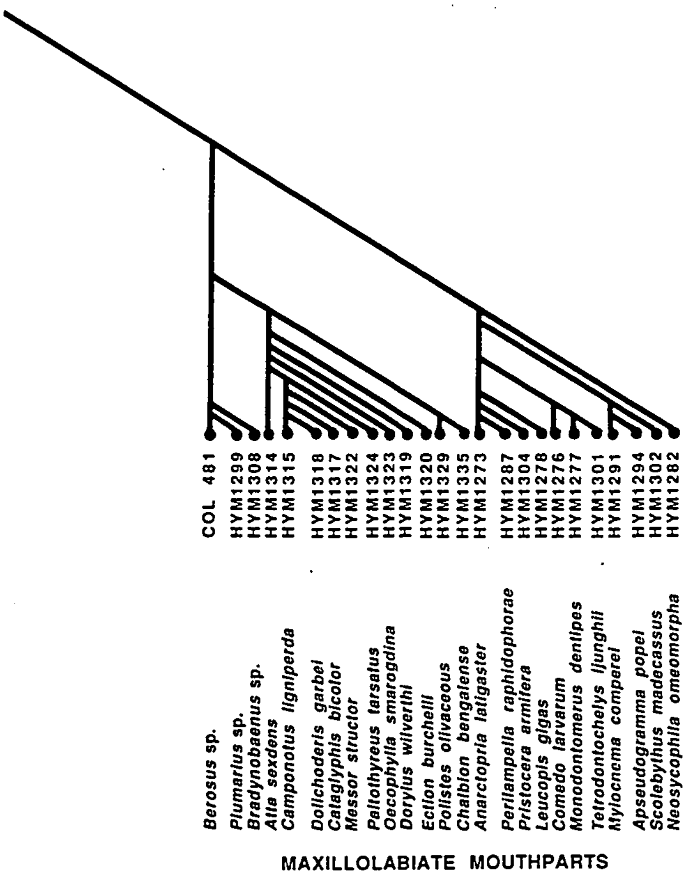


FIGURE 42. Cluster analysis dendrogram of the Maxillolabiate Mouthpart Class. See Fig. 28 for relationships of this mouthpart class to other mouthpart classes.

evidenced by fossils of megalyrids, stephanids and the extinct Ephialitidae (Wootton 1986). Particular apocritan subgroups, such as the Parasitica, are known from proctotrupids and helorids described from Upper Jurassic of the USSR [60] (Kozlov 1968) and the Lower Cretaceous of the USSR and Australia [53,52] (Kozlov 1974, Jell and Duncan 1986). These fossils are followed by a profusion of taxa from Late Cretaceous ambers from Siberia, USSR [37] (Zherikin and Sukacheva 1973) and Canada [35] (Brues 1937) and are represented in Baltic amber [19] (Brues 1937, 1940; Masner 1969). Chalcidoids are traceable to *Galloromma bezonnaisensis* Schlüter 1978 [45] and occur in other Late Cretaceous ambers [40,37,35] but are less well-represented in Tertiary deposits (see Fig. 43 for details).

Aculeate apocritans probably arose during the Late Jurassic since one of the most derived apocritan superfamilies, Sphecoidea, occurs in lowermost Cretaceous strata [57] (Evans 1969). The earliest occurrence of the most plesiomorphic aculeate group, the Chrysidoidea, is Early Cretaceous [53] (Jell and Duncan 1986) and four chrysidoid families are represented in Siberian amber from the Late Cretaceous [37] (Zherikin and Sukacheva 1973), possibly indicating a radiation during the Cretaceous. Tiphioid occurrences include the earliest known form, *Cretavus sibiricus* Sharov 1957, which is probably a mutillid (Rasnitsyn 1980), as well as an undescribed tiphiid from Siberian USSR amber [37] (Zherikin and Sukacheva 1973). Another mutillid is known from Upper Eocene/Lower Oligocene Baltic amber [19] (Brothers 1974). The masarid *Curiovespa curiosa* Rasnitsyn 1975 is from an Upper Cretaceous deposit [39]

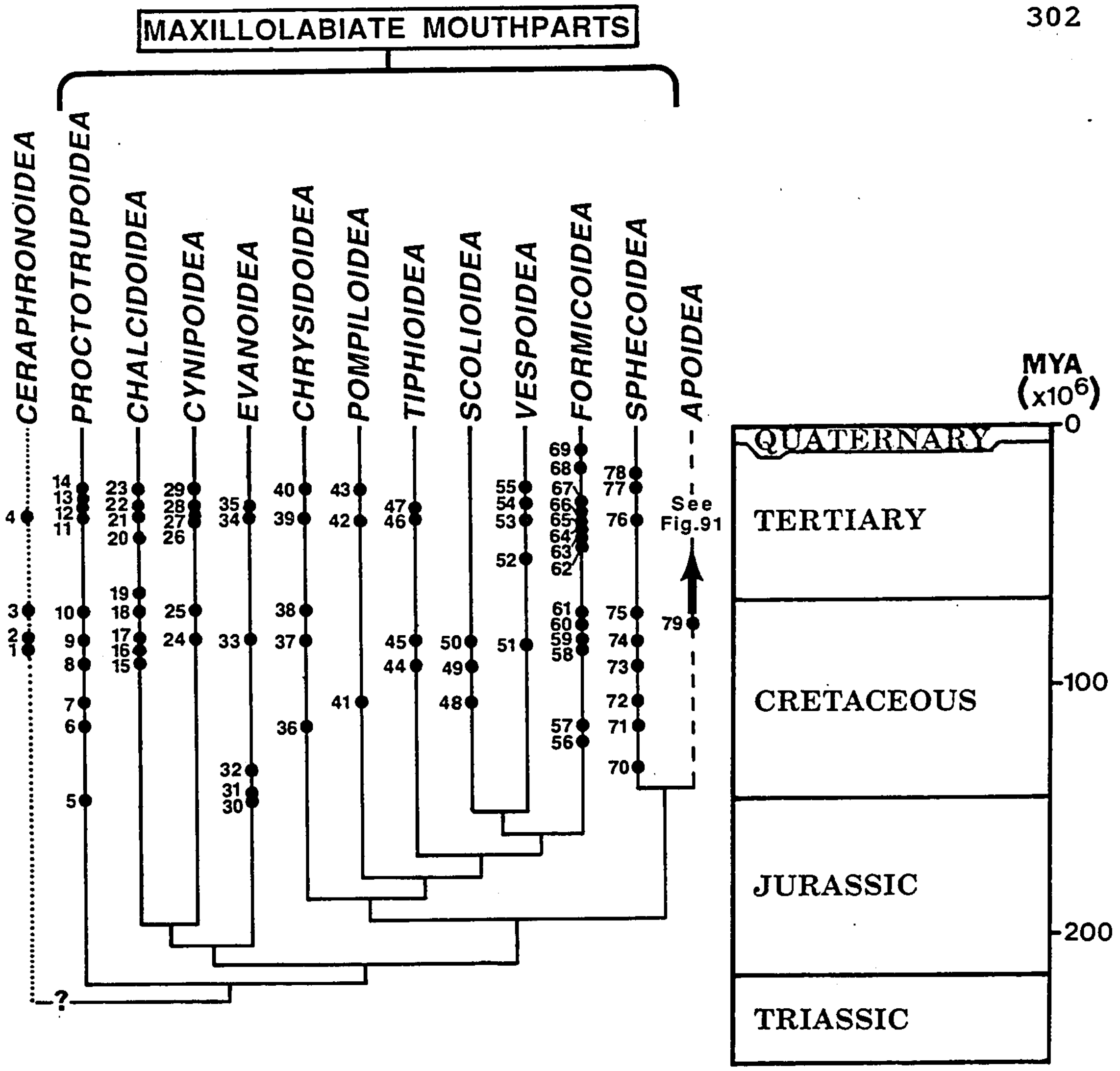


FIGURE 43. Geochronologic history of the Maxillolabiate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Königsmann (1977, 1978a, 1978b). The taxonomic level of analysis is the superfamily. The outgroup is ?Ceraphronoidea. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.

(Rasnitsyn 1975) and an eumenid is known from the Early Eocene of France [27] (Burnham 1978).

Formicids (ants) have a rich fossil record, and though 200 species have been described from many Tertiary deposits (Burnham 1978), only within the last 25 years have Cretaeous ants been known, most of them from amber deposits. The earliest documented ant is from Lebanese amber [55], mentioned by Hennig (1981). Recently Jell and Duncan (1986) described an alate male ant (possibly a nothomyrmecine) from the Lower Cretaceous of Australia [53]. Dlussky (1975) recognized ponerine and sphecomyrmine forms from the Upper Cretaceous of the USSR [37,39] but later re-evaluated his assignments (Dlussky 1983), considering them semisocial and placing them in a new family, the Armaniidae, transitional between scoloid wasps and true ants. Earlier, the first documented fossil ant from the Cretaceous occured in Late Cretacceous New Jersey amber [36]. This fossil, *Sphecomyrma freyi* Wilson and Brown 1967 was described as possessing a mosaic of characters transitional between a tiphioid wasp and modern ants (Wilson 1971) and was placed in a monotypic subfamily, the Sphecomyrminae, within the Formicidae. A similar undescribed form has been recognized in slightly younger amber from Canada [35] (Burnham 1978). Recently Dlussky (1987, 1988) determined that the Sphecomyrminae warranted familial status and, like the Armaniidae, lacked the sociality of true ants because of the absence of certain external structures associated with extant members of the Formicidae. He considers the modern Formicidae as having its origin during the Paleocene. Fossil occurrences of Early Tertiary ants are abundant and have been largely described from the two richest fossil deposits for fossil ants--Upper Eocene/Lower Oligocene Baltic amber [19] (Wheeler 1914) and the Early Oligocene Florissant Formation of Colorado [15] (Carpenter 1930). Both deposits share a taxonomically similar ant fauna.

Previous Designations. Recognition of the structural union of the maxillae and the labium as a single, functioning complex can be traced to Kirmayer's (1909) examination of the mouthparts of *Vespula*, in which it was demonstrated that both mouthpart elements originate from a common region between the mandibles. This region was termed the *Mundfeldsack* by Ulrich (1924). In Bugnion's (1930) monograph on ant mouthparts, the functional integrity of the maxillae and labium was discussed and he referred to the common structure as "*l'appareil maxillo-labial.*" Duncan (1939) described the retractor/protractor musculation of the maxillary complex and Matsuda (1965) provided a comprehensive overview of the mechanics of extension for the maxillolabial complex. Thus the structural and functional uniqueness of the maxilla and labium in apocritan hymenopterans has been firmly established since the early 1900's. (See Table 6 for details on the history of maxillolabiate nomenclature.)

I am adopting the term **maxillolabiate** as a name for the mouthpart class described herein. Although glossates (Section 8.7.2) also have a maxillolabial complex, it is uniquely specialized for the procurement of deeply hidden, fluid food, mostly floral nectar. The glossate maxillolabial complex functions by the characteristic elongation of the glossae and the concomitant development of a tube during galeal apression for squeezing nectar during glossal retraction (Snodgrass 1956). Maxillolabiates, by contrast, lack this mechanism and possess a generalized structure used for food manipulation.

Review of Literature. Sources of data used for maxillolabiate mouthpart structure come from (i) extensive accounts of apocritan hymenopterans, (ii) monographic accounts of selected taxa, in which the mouthparts of a few representative species are mentioned in passing and (iii) works on mouthpart structure of a single or few taxa. Several extensive accounts form a baseline for investigation of maxillolabiates, including Bugnion's (1930) and Gotwald's (1969) extensive and detailed descriptions of ant mouthpart structure, and Brother's (1975) and Osten's (1982) phylogenetic analysis of aculeate and scolioid systematic relationships, in which mouthpart characters were used in part as a basis for assessing relationships among taxa. Other useful studies are ecologically-based examinations by Janvier (1933) of diverse Chilean hymenopterans, Silvestri's (1924) study of the hymenopteran parasites of oak-galling, tortricid parasites, and Smith and Compere's (1928) documentation of the hymenopteran parasites of the homopteran, black scale.

Major monographic studies of hymenoptean taxa with important mouthpart data includes Ferrière's (1929) examination of Javanese chalcidoids for the perilampid *Perilampella raphidophorae* Ferrière, Boucek's (1974) study of the Leucopsidae for *Leucopis gigas* Fabricius, Doutt and Viggiani's (1968) work on the Trichogrammatidae for *Trichogramma popei* Girault, Evans' study of American Bethylidae for *Pristocera armifera* Say, Richards' (1939) study of Britsh Bethylidae for the dryinid *Tetrodontochelys ljunghii* (Westwood) and Yoshimoto's (1984) excellent description of Canadian chalcidoids. Other sources of mouthpart structure data are Bucher (1948) for the chalcid *Monodontomerus dentipes* Boheman, Grandi (1924b) for the torymid *Neosycophila omeomorpha* Grandi, Evans (1966) for the plumariid *Plumarius* sp., Evans (1963) for the scolebythid *Scolebythus madecassus* Evans, Kusnezov (1954b) for the maxillolabial mouthpart structure of two ants, and Smith (1898) and Seghal (1963) for the common vespid *Polistes olivaceus* (DeGeer). Wheeler (1910) and Wilson (1971) provide brief introductions to the head and mouthpart structure of ants. Excellent scanning electron micrographs of ant mouthpart structure are found in Eisenbeis and Wichard (1987) and Whiting et al. (1989).

8.3.7. Raptorial-Ectognathate Class (Class 6)

Description. Head spheroidal to infrequently transversely elongate, nonretractile; proboscis short or uncommonly intermediate to long. Genae and gula moderately to minimally developed. Raptorial prothoracic legs present to assist mouthparts. Antennae setaceous; ocelli 3; compound eyes expansive and holoptic. Mouthparts mandibulate, hypognathous, symmetrical, nonprotractile or protractile (labial mask in some forms). Food pump pharyngeal.

Clypeus transversely elongate, rarely quadrate; subsegmented. Labrum transversely elongate, undivided, with a pectinate margin. Pharynx capacious; hypopharynx lingulate; epipharynx membranous or less commonly setate. Mandibles dicondylic; quadrangular; incisiform;

musculation of adduction/abduction. Maxillae with main-body of four or two sclerites; stipes elongate; bearing a fused palp and mala. Maxillary palp a tapering, unsegmented lobe appressed to mala, of intermediate length. Lacinia fused to galea forming a mala with mesial bristles or setae and a distal raker. Labium with elongate, 2-segmented main-body; bearing a ligula and palps. Main-body segments short and quadrate or vertically elongate and articulating to form a protrusible structure with distal raptorial claws (labial mask). Labial palps chelate, with movable or immovable hooks; 2-segmented; short to intermediate in length. Glossae fused to paraglossae as a generalized ligula. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. Although raptorial-ectognathates are structurally close derivatives of adult-ectognathates, they exhibit a few unique developments. The eyes are very large, often bulging and holoptic, and the antennae resemble setae. While the trophic basket is duplicated in some adult-ectognathates (coleopterans), only in raptorial-ectognathates does it incorporate prothoracic legs as an integral element. The maxillary mala is a fused lacinigalea, consisting of a single, spinose, raptorial structure.

The maxillary palpus is a fleshy, elongate, unsegmented structure adnate to the mala. Fusion of each glossal and paraglossal pair into a glossoparaglossa, in conjunction with transverse expansion of the basal labium, has result in a uniquely broad, platelike labium. Aquatic raptorial-ectognathates (naiads) are the only members, with the exception of some adult staphylinid coleopterans (e.g. *Stenus*), to bear a protrusible and raptorial labial mask for capturing prey.

Diversity and Natural History. Raptorial Ectognathates are obligate insectivores (Hobby 1934, Sih 1987) (Fig. 44) and efficient aquatic and aerial predators (Clausen 1940, Popham and Bevons 1979). Compared to other hexapod mouthpart classes, raptorial-ectognathates are proportionately unimportant, comprising only 0.63% of all species in the modern hexapod fauna (Appendix D). Raptorial-Ectognathates consist of immature and adult odonatans and have a modest diversity, comprising 25 families and about 5,500 species (Appendix D), corresponding to a rank-order of 21 out of 34 mouthpart classes (Table 5, Fig. 131). Raptorial-ectognathate adults are large, conspicuous, predators along streamsides, ponds and other hydric habitats (Richards and Davies 1977), where they frequently form the penultimate or antepenultimate carnivore trophic level. The immatures are aquatic naiads that prey on insect naiads and larvae and other soft-bodied invertebrates using their raptorial labial sling (Pritchard 1976, Merritt and Cummins 1984).

Structural Themes. Raptorial-ectognathates are divisible into three major themes (Fig. 45). The most salient distinction within this odonatan-only mouthpart class is the presence of the unique labial mask among naiads, which is functionally and structurally differentiated from the adult labium. Of the 13 characters that consistently separate members into one of the three themes, 11 of these are associated with the head and mouthpart differences of adults from naiads and six with the special features of the labial mask. (It should be noted that the

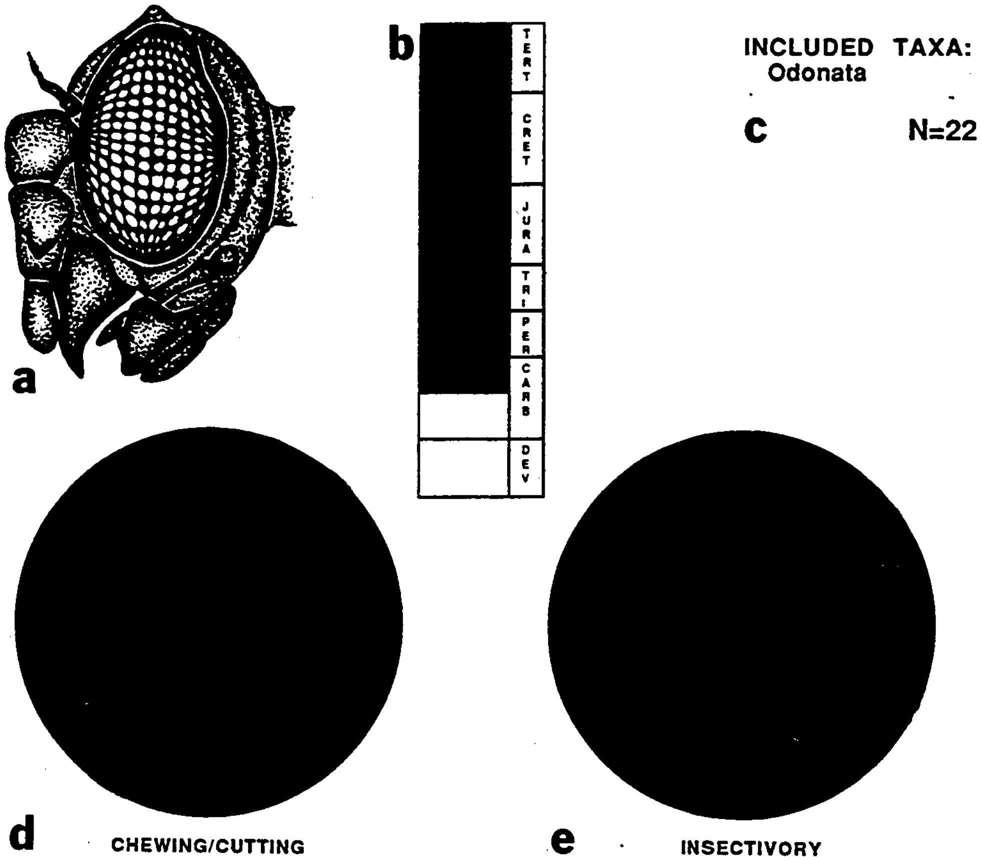


FIGURE 44. Overview of the Raptorial Ectognathate Mouthpart Class. a, *Gomphus agricola* Linneaus (Odonata: Gomphidae, data-set no. 59), after Lew (1933); b, geochronologic range, number of taxa examined; c, taxonomic distribution; d, functional-feeding-group; e, dietary spectrum.

adult coleopteran *Stenus biguttatus* (data-set no. 475), which also has a labial mask-like structure, was not included in this cluster. This is attributable to a relative excess of generalized coleopteran over labial mask character-states.) The 13 characters responsible for the three themes are the following: rostrum/proboscis development, feeding-related modifications, mouthpart placement, clypeal complex shape, labrum shape, labral participation in a multielement mouthpart structure, mandibular type, main-body segmentation of the maxilla, galeal modifications, maxillary participation in a multielement structure, labial palpus type and aspect ratio and labial participation in a multielement structure.

The first theme is demonstrated by Subcluster 1, which comprises 16 adult members from every examined family (in Fig. 45 this subcluster is bracketed by data-set nos. 52 to 72). This subcluster consists of odonatan adults with specialized maxillae and a labium bearing a mentum and submentum of short length and lacking a capacity for protrusibility. Subcluster 2 expresses the second theme and consists only of the adult gomphid *Ictinus angulosus* (data-set no. 61) and is differentiated from other adult gomphids by principally shape-related features such as a quadrate rather than a vertically elongate clypeus, a quadrate rather than a transversely elongate labrum and a equant rather than an elongate labial main-body. Subcluster 3, or the third theme consists of five naiads bracked by data-set nos. 53 to 70 in Fig. 45. This theme is characterized by the unique modifications of the labial sling. Within Subclusters 1 and 3, there is only limited differentiation of taxa, indicating that both themes are highly stereotyped.

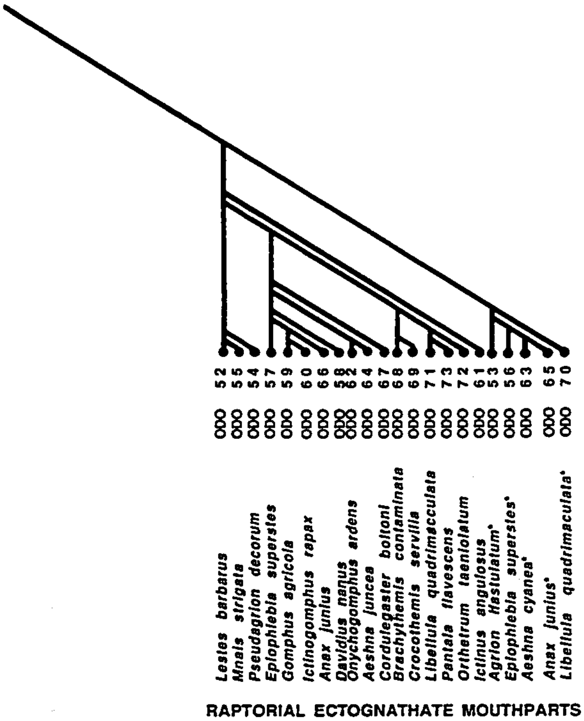

ODO 52 Lestes barbarus
ODO 55 Mnais strigata
ODO 54 Pseudagrion decorum
ODO 57 Epiophlebia superstes
ODO 59 Gomphus agricola
ODO 60 Ictinogomphus rapax
ODO 66 Anax junius
ODO 58 Davidius nanus
ODO 62 Onychogomphus ardens
ODO 64 Aeshna juncea
ODO 67 Cordulegaster boltoni
ODO 68 Brachythemis contaminata
ODO 69 Crocothemis servilia
ODO 71 Libellula quadrimacculata
ODO 73 Pantala flavescens
ODO 72 Orthetrum taeniolatum
ODO 61 Ictinus angulosus
ODO 53 Agrion Hastulatum*
ODO 56 Epiophlebia superstes*
ODO 63 Aeshna cyanea*
ODO 65 Anax junius*
ODO 70 Libellula quadrimaculata*
RAPTORIAL ECTOGNATHATE MOUTHPARTS

FIGURE 45. Cluster analysis dendrogram of taxa comprising the Raptorial Ectognathate Mouthpart Class. See Fig. 28 for relationship of this Mouthpart class to other mouthpart classes.

Geochronologic History. The fossil record of adult raptorial-ectognathates is superior to that of naiad raptorial-ectognathaes. Thus the fossil record of the adult stage forms the basis of the following discussion.

Because of the occurrence of several Carboniferous "suborders" that traditionally have been placed in the Odonata, the earliest Raptorial Ectognathate may be coincident with the appearance of the pterygote record itself whose earliest expression is during the lower Upper Carboniferous of the Upper Silesian coal measures [98] (Hennig 1981, Brauckmann and Zessin 1989). An early form from this deposit, *Erasipteron larischi* Pruvost, has been assigned to the order Protodonata (=Meganisoptera) of the stem-group of the Odonata (Hennig 1981) or to the odonatan suborder Eomeganisoptera (Crowson et al. 1967, Richards and Davies 1977). Protodonatans are dragonfly-like forms with strong mandibles and spiny forelegs (Brauckmann and Zessin 1989) and include some of the largest insects ever (Carpenter and Burnham 1985). However, it is unknown whether they share the unique mandibular, maxillary and labial structure of extant odonatans. I am tentatively considering *Erasipteron* as the earliest member of the raptorial ectognathate class, based on its stem-group membership or annectent association with odonatans, *sensu lato* (for confirmation of this view, see Carpenter 1954). (See Fig. 46 for a summary phylogram and important fossil occurrences of raptorial-ectognathates.)

Demonstrable raptorial-ectognathates make their appearance during the Lower Permian, although most forms are dimunitive when compared to

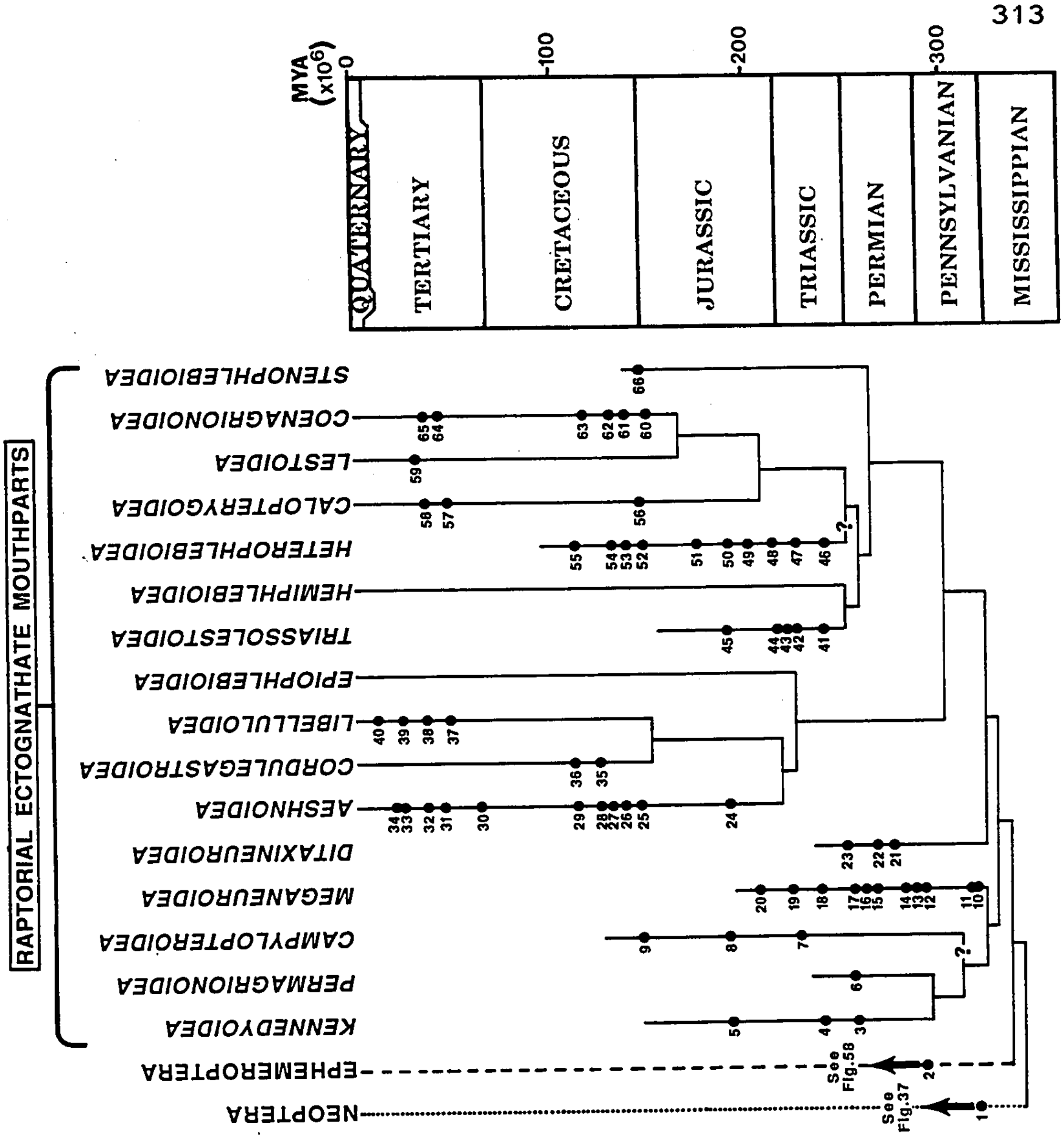


FIGURE 46. Geochronologic history of the Raptorial Ectognathate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Pritykina (1980), Hennig (1981) and Brauckmann and Zessin (1989). The taxonomic level of analysis is the superfamily. The outgroup is Ephemeroptera; the relationship of Neoptera to Odonata + Ephemeroptera is also indicated. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.

modern forms (Carpenter 1931, 1947). Members of the extinct odonatan suborders Protanisoptera and Protozygoptera are found in upper Lower Permian sediments [90] of Kansas (Tillyard 1925, Crowson et al. 1967). A zygopteran has been documented from Upper Permian rocks of the Malvinas/Falklands Islands [85], although more specific stratigraphic correlation is uncertain. In many instances the odonatan affinities of these Permian fossils are assigned on the basis of wing venation and body form; mouthparts are rarely available and thus the associations of modern and Permian Raptorial Ectognathates arises from wing homologies.

Previous Designations. Previous recognition of raptorial-ectognathate mouthparts was possibly made by Metcalf et al. (1962: 141) in his "grasping or predaceous subtype" of his "chewing type" (Table 6), a designation which could apply to either the adult or naiad members of raptorial-ectognathates. However the examples that Metcalf used were adult coleopterans with prominent, sickle-shaped mandibles and not adult odonatans. Usually the term "mandibulate" or similar general terminology has been used to characterize what is herein designated as **raptorial-ectognathate** mouthparts.

Review of Literature. Individual accounts documenting adult raptorial-ectognathate mouthparts and head structure include those of Strenger (1952) for the lestid *Lestes barbarus* (Fabricius), the massive monograph of Asahina (1954) for the rare, relict anisozygopteran *Epiophlebia superstes* Selys, Mathur and Mathur (1961b) for the gomphid *Ictinus angulosus* Selys, Chao (1953) for the gomphid *Onychogomphus ardens* Needham, Short (1955) for the aeshnid *Aeshna cyanea* Müller, Smith and Pritchard (1956) for the cordulegasterid *Cordulegaster boltoni* (Donovan), Mathur (1956) for the libellulid *Brachythemis contaminata* Fabricius, Mathur and Mathur (1961a) for the libellulid *Orthetrum taeniolatum* Schneider, and Mathur (1962) for the libellulid *Pantala flavescens* Fabricius. This descriptive work was primarily done during the 1950's and 1960's. Reviews of adult odonatan structure, particularly mouthparts and the head, can be found in Butler (1904, labia only), Lucas (1923/24, mostly labia), Lew (1933, mostly head structure) and Hakim (1964, all structures). Popham and Bevons (1979) have presented a functional-morphological account of the feeding mechanism for *Aeshna juncea* Linneaus.

There has been fewer studies on the mouthpart and head structure of raptorial-ectognathate immatures. Descriptions of naiad odonatans include the anisozygopteran *Epiophlebia superstes* Selys by Asahina (1954), and among the anisopterans, the aeshnids *Aeshna cyanea* Müller by Short (1955) and *Anax junius* (Drury) by Snodgrass (1954), and the libellulid *Libellula quadrimaculata* Linneaus by Pritchard (1976). Other sources of mouthpart and head data include Lucas (1923/1924, labia only), Watson (1925, mandibular dentition), Lew (1933, all structures), Grieve (1937, stomodael muscles) and Corbet (1953, labia only).

Considerable attention has focused on the naiad labium because of (i) considerable debate concerning the dynamics of the strike mechanism and (ii) its peculiar structural transformation into the adult labium during development. Accounts documenting the strike mechanism are Watson (1955), Caillère (1972), Pritchard (1976), and Tanaka and Hisada (1980). Studies documenting the metamorphosis of the labium from the naiad to the adult are older and include Butler (1904), Whedon (1927), Munscheid (1933) and Corbet (1951).

8.3.8. Mortar-and-Pestle Class (Class 7)

Description. Head spheroidal, nonprotractile, nonproboscate or with a short proboscis. Genae prominent or well developed; gula well developed or absent. Antennae filiform or capitate; ocelli 3 or absent; compound eyes moderately developed and dichoptic, or absent. Mouthparts mandibulate, hypognathous or prognathous, symmetrical or with single element asymmetry, nonprotractile. Food pump clypeal.

Clypeus quadrate to vertically elongate, often bulging; undivided or divided into 2 sclerites. Labrum vertically elongate, rarely quadrate; undivided; with straight to pectinate margin. Pharyngeal region capacious; hypopharynx bearing a basal sitophore, two lateral ovoidal sclerites and superlingulae; epipharynx molariform or less commonly membranous. Mandibles dicondylic; tetragonal in shape; molariform or incisiform, rarely caniniform; musculation for adduction/abduction. Maxilla with 1 basal sclerite as main body; stipes equant to infrequently elongate; bearing galea and lacinia, with or without a palpus. Maxillary palpus rarely absent; when present serrate or filiform-moderately clavate, 4-segmented and of variable length. Galea palpiform or a lobate rasp; lacinia a maxillary pick. Labium with elongate main-body of 3 or 2 segments; bearing glossae, paraglossae and labial palps, or labial palps only. Labial palpus papillate or clavate; 1-segmented or infrequently 2- segmented; short in length. Glossae often fused to paraglossae to form a ligula; when separate glossae bearing silk glands or papillate and paraglossae lingulate or a generalized fleshy lobe. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. Several unique features are diagnostic of the Mortar-and-Pestle Class. Members of this class are the only forms uniquely to combine a large, well-developed clypeal pump with mandibulate mouthparts. They also possess a unique hypopharynx that, on its dorsal surface bears a mortar-like depression to accomodate a projecting epipharyngeal pestle-like process. The hypopharynx also uniquely bears two, projecting, ovoidal sclerites for reception in two labial sulci. A third diagnostic feature is the maxillary pick. Labial palpi are reduced to one, rarely two, segments. The combination of an epipharyngeal/hypopharyngeal mortar-and-pestle apparatus and a lacinial pick, constitutes a unique feeding apparatus.

Diversity and Natural History. In terms of the total diversity of mouthpart classes, the Mortar-and-Pestle Class is taxonomically insignificant, accounting for approximately 0.7% of extant species diversity (Appendix D). Mortar-and-pestle members are psocopterans and mallophagans except for haematomyzids. The mouthpart class has only a modest diversity, comprising 48 families, 482 genera and about 5,500 species (Appendix D), translating to a rank-order of 19 out of 34 mouthpart classes (Table 5, Fig. 131).

Mortar-and-pestle forms are dietarily characterized mainly by necrovory (Fig. 47)--feeding on dead plant, animal or fungal material,

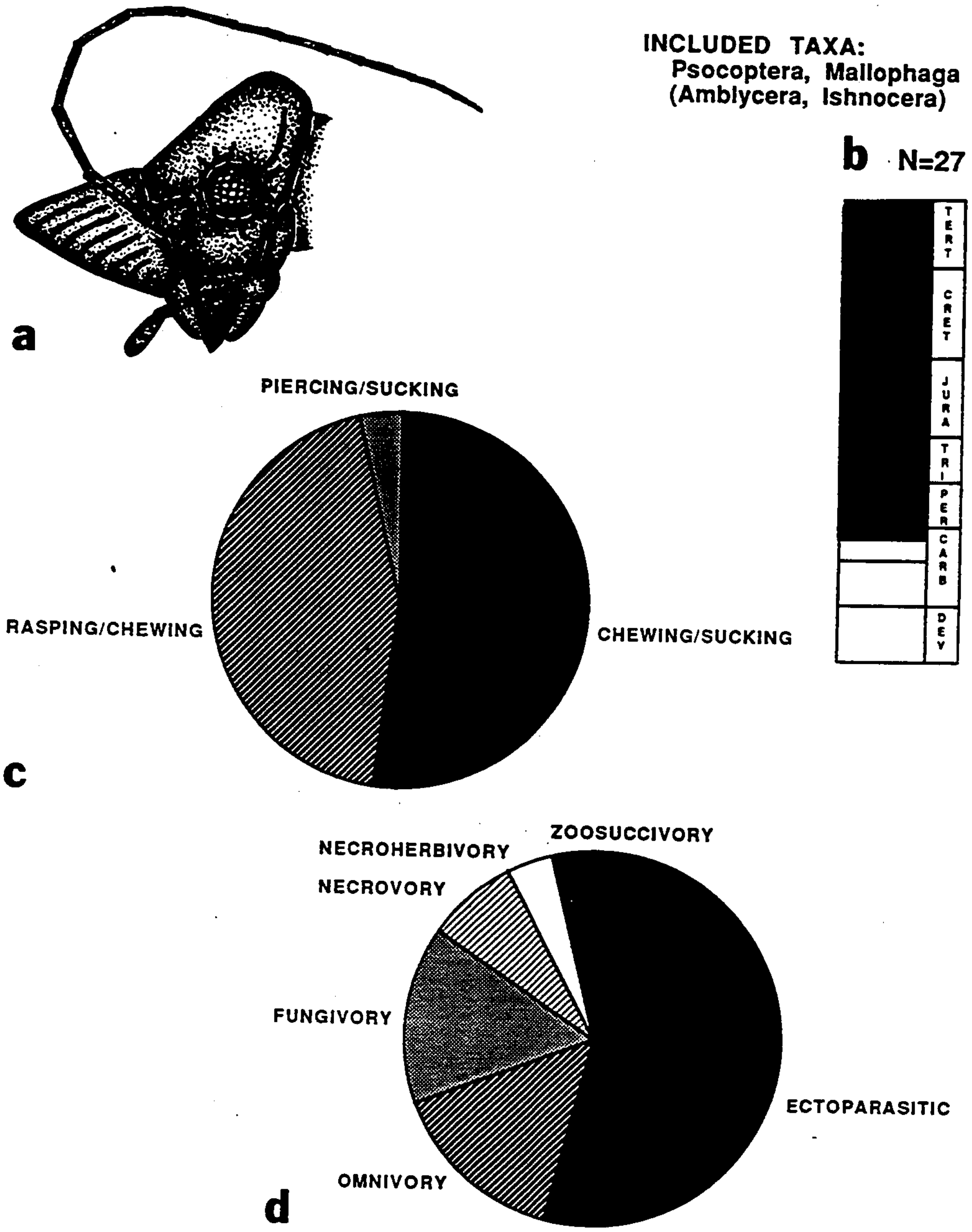


FIGURE 47. Overview of the Mortar-and-Pestle Mouthpart Class. a, *Rhinopsocus arduus* Badonnel and Lienhard (Psocoptera: Mesopsocidae, data-set no. 190), after Badonnel and Lienhard (1988); b, taxonomic composition, number of taxa examined and geochronologic distribution; c, functional-feeding-groups; d, dietary spectrum.

such as litter, bark flakes, wood, or exudates; they are less commonly microvores--feeding on live yeast, algae, spores and pollen (Waage 1979, New 1984, Lawrey 1987, Marshall 1987 and references therein). They are characterized by two major life-habit tendencies, occurring on arboreal and ground habitats where plant decomposition is present (Badonnel 1951, New 1984) and particularly bark habitats (Hamilton 1978); and as mostly feather-, skin-, and exudate-consuming ectoparasites on mammalian and avian hosts (Waage 1979, Marshall 1987). Active predation has been rarely documented for mortar-and-pestle members (New 1984). Generally, members of this mouthpart class are small inconspicuous, inhabiting protected, cryptic habitats, and are either flightless or weak fliers.

Structural Themes. The Mortar-and-Pestle Class exhibits two pronounced subclusters (Fig. 48). These two, discrete subclusters are congruent with the two major taxa that constitutes the mouthpart class: psocopterans form Subcluster 1 and nonhaematomyzid mallophagans form Subcluster 2. These two themes are clearly defined by 18 characters, most of which separate the two subclusters by mutually exclusive character-states. (This clear-cut dichotomy contrasts with the high degree of character-state comingling among the subclusters of the Sericterate Mouthpart Class [Section 8.3.14].) The 18 characters represent an eclectic sampling from all head and mouthpart regions. The characters are rostrum/proboscis development, gula/hypostome development, antennal type, ocellar presence, compound eye condition, mouthpart placement, mouthpart symmetry, clypeal complex shape, clypeal subsegmentation, labral participation in a multielement mouthpart structure,

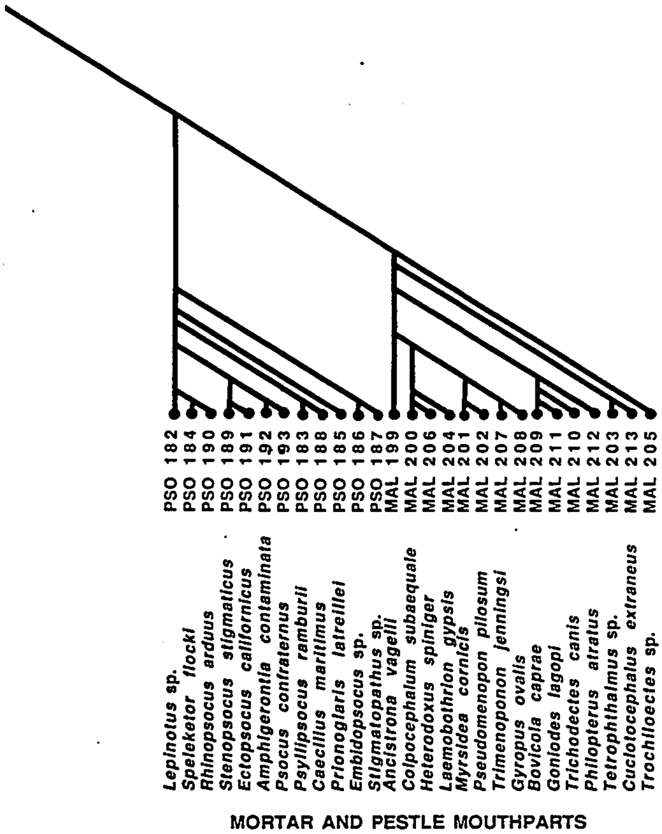

Lepinotus sp. PSO 182
Speleketor flocki PSO 184
Rhinopsocus arduus PSO 190
Stenopsocus stigmaticus PSO 189
Ectopsocus californicus PSO 191
Amphigerontia contaminata PSO 192
Psocus contraternus PSO 193
Psyllipsocus ramburii PSO 183
Caecilius maritimus PSO 188
Prionoglaris latreillei PSO 185
Embidopsocus sp. PSO 186
Stigmatopathus sp. PSO 187
Ancistrona vagelli MAL 199
Colpocephalum subaequale MAL 200
Heterodoxus spiniger MAL 206
Laemobothrion gypsis MAL 204
Myrsidea cornicis MAL 201
Pseudomenopon pilosum MAL 202
Trimenoponon jenningsi MAL 207
Gyropus ovalis MAL 208
Bovicola caprae MAL 209
Goniodes lagopi MAL 211
Trichodectes canis MAL 210
Philopterus atratus MAL 212
Tetrophthalmus sp. MAL 203
Cuclotocephalus extraneus MAL 213
Trochiloecetes sp. MAL 205
MORTAR AND PESTLE MOUTHPARTS

FIGURE 48. Cluster analysis dendrogram of taxa comprising the Mortar-and-Pestle Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

epipharyngeal type, mandibular dentition, maxillary palpus type, maxillary palpus aspect-ratio, galeal modification, shape of the labial main body, glossal modification and paraglossal modification.

Cluster 1 consists of dominately free-living psocopterans (bracketed by data-set nos. 182-193 in Fig. 48) with robust heads bearing filiform antennae, hypognathous mouthparts, a expansive clypeus and typical, tetragonal mandibles with molar and incisor regions. Cluster 2 (data-set nos. 199 to 205) consists of ectoparasitic mallophagans with a dorsoventrally flattened head that bears capitate antennae housed in scrobes, prognathous mouthparts, a de-emphasized clypeus and edentate, psittaciform mandibles. Although these distinctions are many, this mouthpart class nevertheless is integrated by the joint presence of structures such as the lacinial pick and the characteristic mortar-and-pestle complex of the hypopharynx and epipharynx. The mallophagan *Haematomyzus elephantis* is a member of the Buccal Cone Mouthpart Class (Section 8.9.3).

Geochronologic History. The earliest candidate for membership in the Mortar-and-Pestle Class is *Gerarus danielsi* Handlirsch, from the Upper Carboniferous of Illinois [96]. This form, assigned to the order Protorthoptera (see Burnham 1983 for systematic placement) is mandibulate and has an evident clypeal pump (Kukalová-Peck 1987, fig. 18). Details of its hypopharynx and maxilla are unknown (Burnham 1983; Labandeira, pers. observ.).

By the Lower Permian the earliest known psocopterans appear in siltstones of central Kansas [90] and the Perm region of the USSR [89]

(Carpenter 1932, 1933; Martynova 1928) (Fig. 49). Most of these forms are assigned to the Suborder Permopsocoptera (Tillyard 1926, Carpenter 1954) and lack the head and mouthpart features that uniquely define the Mortar-and-Pestle Class. One well-preserved form from central Kansas, *Dichentomum tinctum* Tillyard 1926, in fact has mouthpart and head features closely resembling the Rostrate Class. However, other Permopsocida, such as *Delopterum minutum* Sellards, bear nonrostrate crania (Tillyard 1928) and are probably members of the mortar-and-pestle class. In a differing interpretation, Zalessky (1937) maintained that at least some of these forms possessed psocopteran rostrate crania, but with homopteran-type sucking mouthparts; and they were accordingly assigned to the newly-created Hemipsocoptera. Carpenter (1938), however, clarified this assignment by demonstrating that Zalessky's material consisted of archescytinid homopterans.

The Permopsocida occur in Mesozoic deposits and are documented from the Middle Jurassic of China [64] (Hong 1983) and the Lower Cretaceous of Australia [53] (Jell and Duncan 1986). These forms characteristically lack an inflated clypeus and bear dorsoventrally prolonged heads with subterminal mouthparts (Carpenter 1933, fig. 13 and plate 1, fig. 2).

The first appearance of undoubted members of the Mortar-and-Pestle Class occur in Upper Cretaceous amber from the Taimyr Peninsula of the USSR [37] (Vishniakova 1975) and from the Late Cretaceous of Cedar Lake, Manitoba, Canada [35] (McAlpine and Martin 1969). Probable Lower Cretaceous representatives occur in Lebanese amber [55] (Schlee and

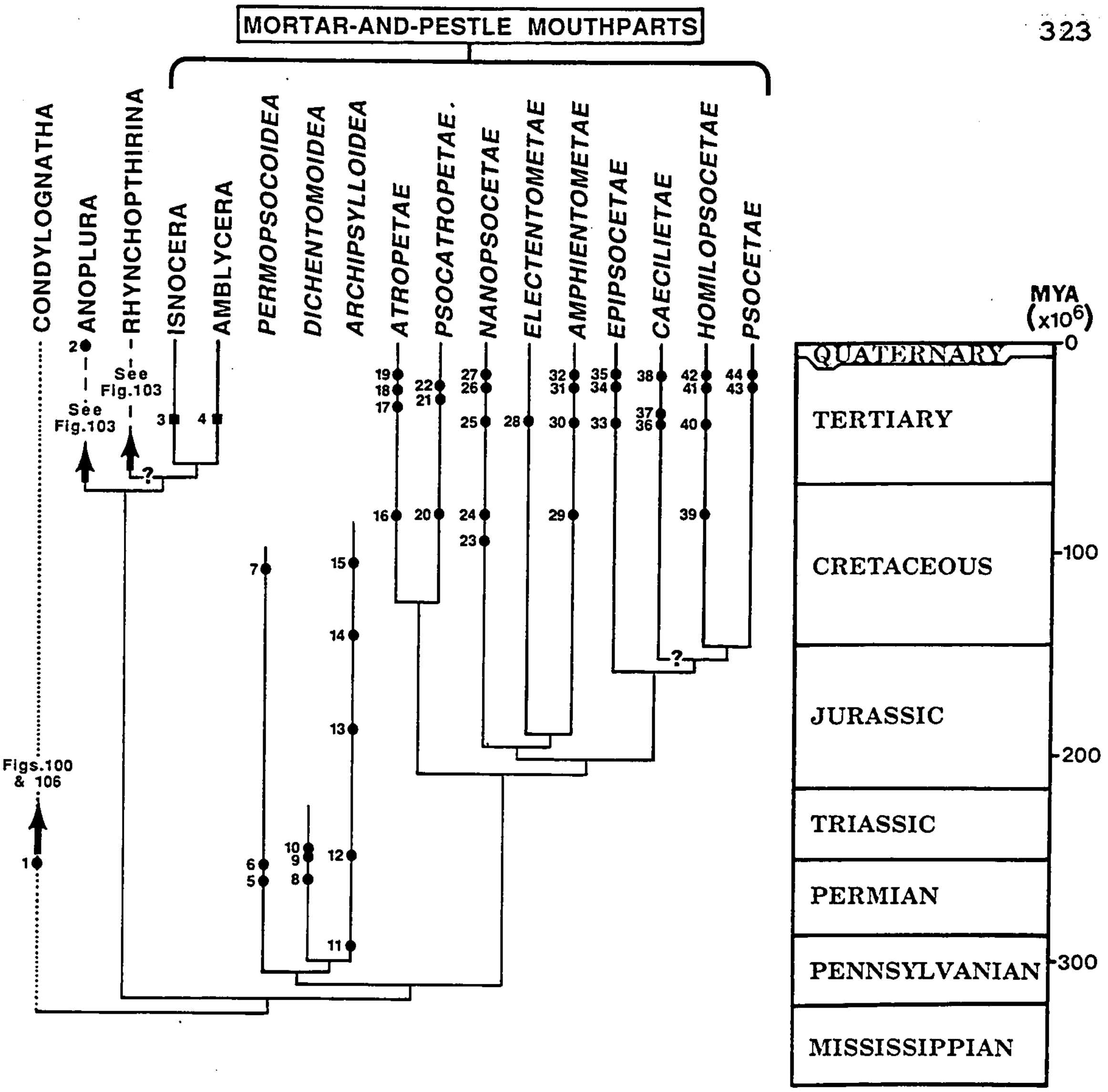


FIGURE 49. Geochronologic history of the Mortar-and-Pestle Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Smithers (1972), Vishniakova (1980), Hennig (1981) and Jamieson (1987). The taxonomic level of analysis is the superfamily and suborder. The outgroup is Condylognatha (=Thysanoptera + [Homoptera + Heteroptera]). These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.

Dietrich 1969) but are undescribed. By the Paleogene, mortar-and-pestle forms are diverse, well-established and are documented by psocid species from Burmese, Baltic [19], and Chiapas [11] ambers (Cockerell 1916, 1919; Kolbe 1883, Enderlein 1911, Navas 1914 and Mockford 1969, respectively). These Upper Cretaceous to Recent forms bear mouthpart and cephalic features typical of the mortar-and-pestle class, and contrast sharply with the Permopsocida, which probably became extinct during the Cretaceous. Mallophagan representatives of the Mortar-and-Pestle Class have a poor fossil record (see Keilbach 1982 for a probable occurrence).

Previous Designations. The term "mortar-and-pestle" was used by Weber (1933, 1936), in the German, to describe unique structures occluding between the epipharynx and hypopharynx. Other than subsequent references to this hypopharyngeal structure in psocopterans and mallophagans, no term has been applied to describe either this unique mouthpart structure or the more general mouthpart and head type. Generally, mortar-and-pestle mouthparts have been considered under more general categories such as the "chewing type" of the "Mandibulate Series" (Metcalf 1929), "orthopteran type" (James and Harwood 1969), or "chewing type" (Ross et al. 1982). (See Table 6 for a history of nomenclature.) The descriptive term **mortar-and-pestle** refers to a diagnostic mouthpart feature as a name for this well-integrated mouthpart group.

Review of Literature. There are few monographic descriptions of the mouthpart and head structure of mortar-and-pestle forms, particularly psocopterans. Reviews of the mouthpart and head structure of an eclectic sampling of mortar-and-pestle forms are provided by Snodgrass (1905, 1944), Weber (1938a) and Symmons (1952). For psocopterans, Burgess (1878) and Borner (1929) briefly describe the head and mouthpart structure of the psocid *Psocus*, Badonnel (1936a, 1936b) discusses the mouthparts of several species, and Cope (1940) provides a description of the head and mouthparts of *Psocus confraternus* Banks. Interesting accounts are given by Ball (1936) and Gurney (1943), who describe major structural transformations in the mouthparts of *Prionoglaris stygia* Enderlein between the nymphal and adult stages.

Mallophagan head and mouthpart structure have received better documentation. The heads and mouthparts have been described for the menoponid *Myrsidea cornicis* (DeGeer) by Buckup (1959), for the menoponid *Pseudomenopon pilosum* (Scopoli) by Haub (1967), for the menoponid *Tetrophthalmus* sp. by Cope (1951), for the trimenoponid *Trimenopon jenningsi* Kellogg and Paine by Stowe (1943) and for the bovicolid *Bovicola caprae* (Gurlt) by Risler (1951). Most of these studies were done in the German school of functional morphology.

8.3.9. Rostrate Class
(Class 8)

Description. Head vertically prolonged with a short to long proboscis (rostrum); nonprotractile. Genae expansive; gula moderately developed but also well-developed or absent. Antennae filiform; ocelli 3 or rarely absent; compound eyes expansive, rarely moderately developed. Mouthparts mandibulate, hypognathous, symmetrical, nonprotractile. Food pump clypeolabral.

Clypeus quadrate, rarely otherwise; undivided and separate or fused to the labrum. Labrum variously shaped; undivided or fused to clypeus; with straight to shallowly curvilinear or broadly acute margin. Pharyn-geal region capacious; hypopharynx lingulate; epipharynx bearing two sclerotized rods, or rarely membranous. Mandibles dicondylic; prolonged or ensiform, rarely otherwise; serrated or incisiform; musculation of adduction/abduction. Maxilla with main-body of 2 sclerites; stipes rodlike; bearing galea, lacinia and palpus. Maxillary palp filiform and moderately clavate; 5-segmented; long to very long. Galea palpiform or penicillate; lacinia penicillate or rarely pectinate, with mesially-directed setae. Labium with an equant main-body of 2 segments; bearing labial palps only. Labial palps filiform, rarely with an enlarged middle segment; 2- or rarely 3-segmented; length variable. Glossae absent or rarely a flabellate tongue; paraglossae absent. Interrgional co-optation of mouthpart elements absent.

Key Phenocharacters. Diagnostic rostrate features include the co-optation of cephalic capsule wall sclerites to form a hypognathously prolonged rostrum. The mouthparts are accordingly elongated with rodlike elements. (This is in contrast to the exclusively terminally attached, unelongated elements of rhynchophorates [Class 9].) A distinctive facial sclerite occurs by the fusion of the frons, clypeus and labrum. The characteristic labium features a nonligulate, elongated base bearing two-segmented palpi with robust, ovoidal segments.

Diversity and Natural History. The Rostrate Class is depauperate in species when compared to other mouthpart classes. Rostrates comprise

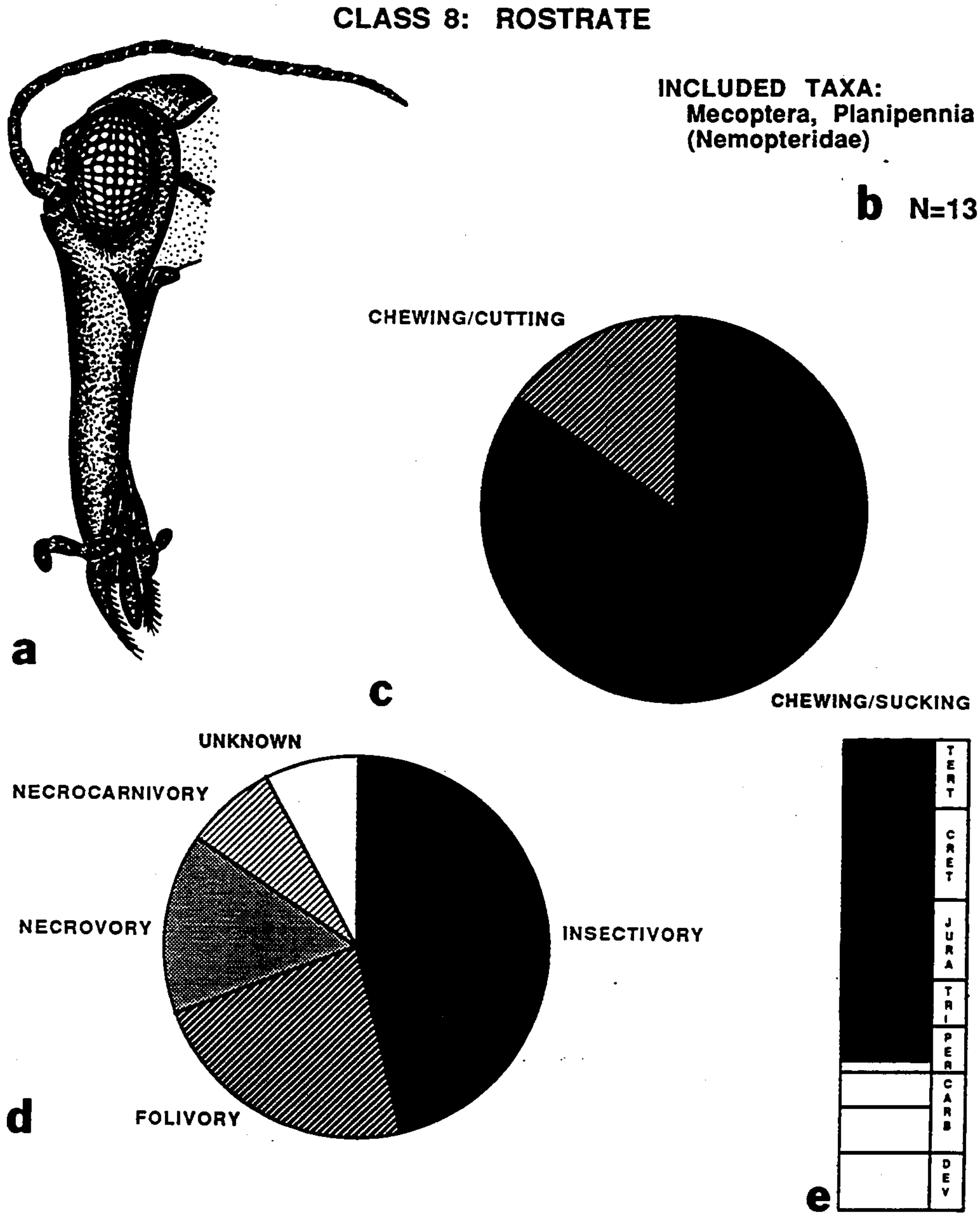


FIGURE 50. Overview of the Rostrate Mouthpart Class. a, *Panorpa nuptialis* Gerstaecker (Mecoptera: Panorpidae, data-set no. 764), after Ferris and Rees (1939); b, taxonomic distribution and number of taxa examined; c, functional-feeding-groups; d, dietary spectrum; e, geochronologic range.

only 0.07% of extant insect diversity and consist of eight families, about 70 genera, and about 600 species (Appendix D). This corresponds to a rank-order of 29 among 34 mouthpart classes (Table 5, Fig. 131). This depauperate taxonomic and ecological representation is in sharp contrast with fossil mecopterans, which are proportionately more diverse in local insect deposits (Whalley 1985), often comprising 20% of all insects found in some deposits (Tillyard 1926). Rostrates currently comprise the adult members of the "generalized" holometabolous orders Planipennia (nemopterids only) and Mecoptera (all forms except nannochoristids), both of which may be phylogenetically related (Boudreaux 1987).

Because of their relative rarity in the modern fauna, secretive habits and probable low numbers of mecopterists, little is known about rostrate diets. Dietary generalizations about the group appear conflicting. According to Setty (1940) and Whalley (1985), adult mecopterans are "mostly carnivorous." This differs from other natural historical accounts provided by Carpenter (1931), Hobby and Killington (1934) and Heddergott (1938), which consider most species necrovores, rarely predaceous. As a mouthpart class, rostrates appear to be omnivorous (Fig. 50).

Structural Themes. Rostrates exhibit three taxonomically nondiverse subclustering patterns, or themes (Fig. 51). Ten characters consistently define these three themes. They are ocellar number, clypeal complex shape, epipharyngeal type, mandibular dentition, lacinial and galeal modifications, labial palpus type and segmentation,

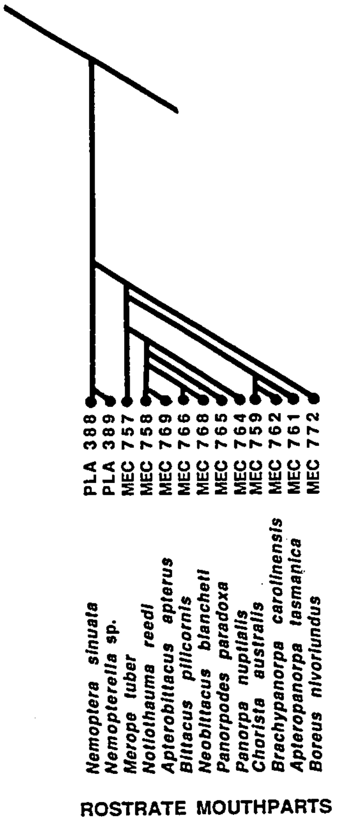
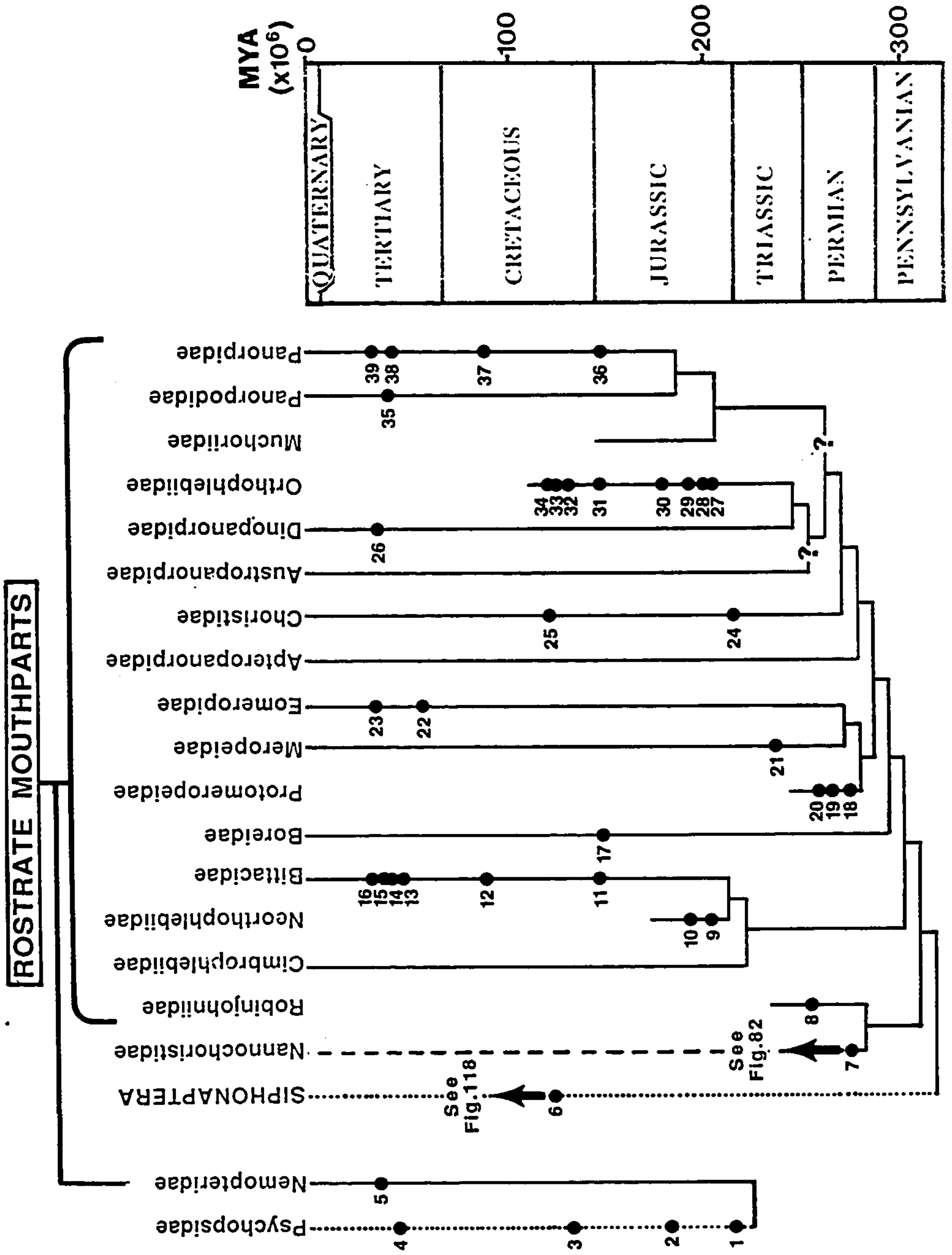

PLA 388 Nemoptera sinuata
PLA 389 Nemopterella sp.
MEC 757 Merope tuber
MEC 758 Notiothauma reedi
MEC 769 Apterobittacus apterus
MEC 766 Bittacus pilicornis
MEC 768 Neobittacus blanchei
MEC 765 Panorpodes paradoxa
MEC 764 Panorpa nuptialis
MEC 759 Chorista australis
MEC 762 Brachypanorpa carolinensis
MEC 761 Apteropanorpa tasmanica
MEC 772 Boreus nivoriundus
ROSTRATE MOUTHPARTS

FIGURE 51. Cluster analysis dendrogram of taxa comprising the Rostrate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

and glossal modifications. Among the three themes, all of these 10 characters discriminate nemopterids from mecopterans, but only four differentiate *Boreus novoriundus* from all other adult mecopterans. The adult mecopteran *Nannochorista dipteroides* is a member of the Labellate Mouthpart Class (Section 8.5.3). Subcluster 1 comprises two adult planipennian genera, the nemopterids *Nemoptera sinuata* and *Nemopterella* sp. (data set taxa 388 and 389). These taxa are structurally convergent with mecopterans in several respects, particularly head capsule shape, but sufficiently disparate in mouthpart structure that they are a separate subcluster. Nemopterids possess a generalized labium that includes a ligula and three-segmented palps. Subcluster 2 (bracked by data-set taxa 757 to 761) are typical mecopterans with elongate, hypognathous mouthparts borne at the base of a prominent rostrum and an aligulate labium with two-segmented palps. By contrast Subcluster 3 consists only of *Boreus nivoriundus* (772) which bears more generalized, unmodified mouthparts, a dimunitive maxillary palp and a unique condition of basal maxillary sclerites for the mouthpart class.

Geochronologic History. The earliest documented rostrate is the promeropeid *Tomiochorista nubila* Martynova from the Lower Permian deposits of the Kusnetsk Basin, USSR [97] (Fig. 52). Slightly younger, Lower Permian forms [90] assigned to the Mecoptera were described by Tillyard (1926) and Carpenter (1930). It is unclear whether these early mecopterans, taxonomically referred to the extinct suborder Protomecoptera, are rostrates since virtually all of the examined fossil material are wings. However, *Permopanorpa inaequalis* Tillyard is reconstructed

FIGURE 52. Geochronologic history of the Rostrate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Withycombe (1924) and Henry (1982). The level of taxonomic analysis is the family. The outgroups are Psychopsidae and Siphonaptera. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.


MYA
(x10^6)
0
100
200
300
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
PENNSYLVANIAN
Panorpidae
Panorpodidae
Muchoriidae
Orthophlebiidae
Dinopanorpidae
Austropanorpidae
Choristidae
Apteropanorpidae
Eomeropidae
Meropeidae
Protomeropeidae
Boreidae
Bittacidae
Neorthophlebiidae
Cimbrophlebiidae
Robinjohniidae
Nannochoristidae
SIPHONAPTERA
Nemopteridae
Psychopsidae
ROSTRATE MOUTHPARTS
See Fig.82
See Fig.118
?
?
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39

with a discernable, albeit short, rostrum (Carpenter 1930, fig. 3b). Hennig (1981), however, claims that these forms are unassignable to the order and could equally well be plausible members of the stem-group of the Diptera. Somewhat younger, reliably identified mecopterans are *Nannochoristella reducta* Riek and *Neochoristella optata* Riek from the Upper Permian Belmont beds of Australia [83] (Riek 1953). However, they are assigned to the Nannochoristidae, and since adult nannochoristids are members of the labellate mouthpart class (Section 8.5.3), they are excluded as rostrates.

Rostrates are plentiful in most Mesozoic, insect-bearing deposits and are represented predominately by wings. Mesozoic rostrates are mostly members of the widespread mecopteran family Orthophlebiidae. They are found in the Middle Triassic of Australia [80] (Riek 1950), the Early Jurassic of England [69] (Tillyard 1933, Whalley 1985) and the Lower Cretaceous of Victoria, Australia [53] (Jell and Duncan 1986). These Mesozoic specimens are preserved in fine-grained clastic sediments, occasionally with preserved heads, leading Whalley (1985: 150) to comment, with regard to the Jurassic British material that:

> There is no reason to suppose, from a study of the few preserved mouthparts of fossil Mecoptera, that their feeding habits were any different from those of their living relatives.

Tillyard (1933: 23), in an earlier diagnosis of the family Orthophlebiidae, described the head as "... very small, rostrum moderately developed ..."

The geochronologic history of nemopterid rostrates is depauperate (Fig. 52) since the earliest and only fossil occurrence is from the

Oligocene of the US [15] (Carpenter 1960a). The probable sister-group to the Nemopteridae, the Psychopsidae, is better documented and has an earliest occurrence in the Late Permian of the USSR [74] (Tillyard 1922), indicating a long and unrecognized history for nemopterids.

Previous Designations. The term "rostrum" has been frequently used to refer to the highly stereotyped prolongation of the head in adult mecopterans (Issiki 1933, Hepburn 1969) and adult nemopterid planipennians (Acker 1958, Picker 1987). This term has also been used for designating other elongated, mouthpart-bearing head structures, including the characteristic snout of curculionoids (Morimoto 1962), the beak of heteropterans (Ekblom 1926) and the proximal proboscis of dipterans (Hewitt 1907). In a general sense, any food-related prolongation of the insectan head has often been termed a "rostrum" (Torre-Bueno 1985). Historically, rostrate mouthparts have been considered a subset of mandibulate mouthparts (Table 6). Chaudonneret (1983) has use the term, *rostre*, to refer to a distinctive mouthpart type that includes both mecopterans and curculionids and is characterized by elongation of the cephalic capsule. I am borrowing his terminology and thus the term **rostrate** to refer to this mouthpart class, although I am excluding weevels (see Section 8.4.6).

Review of Literature. Rostrate mouthpart and head structures have been adequately described by a few reviews and several sources documenting particular species. Review articles describing various mecopterans from several families include Otanes (1922), Matsuda (1965) and Hepburn (1969). Detailed descriptions include that of Setty (1940) for the bittacid *Bittacus pilicornis* Westwood, Heddergott (1938) and Ferris and Rees (1939) for the panorpids *Panorpa communis* Linneaus and *P. nutialis* Gerstaecker, respectively, and Issiki (1933) for the panorpodid *Panorpodes paradoxa* MacLachlan. The nemopterid planipennians *Nemopterella* sp. and the bizarre *Palmipenna aeoloptera* Picker are described by Acker (1958) and Picker (1987), respectively. Imms (1944) discusses the homologies of the maxillae and labium of several mecopteran and dipteran species.

8.3.10. Rhynchophorate Class
(Class 9)

Description. Head anteriorly prolonged to less frequently spheroidal; proboscis long to infrequently short; nonprotractile. Genae expansive to well-developed; gula elongated into a pregula, or moderately developed. Mouthparts mandibulate, hypognathous, nonprotractile, with single element asymmetry. Food pump clypeal and pharyngeal.

Clypeus mostly quadrate, uncommonly transversely elongate; undivided or fused to frons; rarely absent. Labrum absent. Hypopharynx a lingulate lobe; epipharynx membranous, setate, or rarely lobate. Mandibles modified dicondylic; ratchet-shaped or tetragonal; incisiform; musculation involved in modified adduction/abduction. Maxillae comprising two sclerites; stipes equant; bearing a galea, lacinia and palpus, often with galea and lacinia fused into a mala. Maxillary palps mucronate or stubby, rarely filiform; 1- to 4-segmented; short in length. Galea mostly penicillate or a mala of mesial pectinate bristles and a distal raker; lacinia penicillate or fused together as a mala.

Labium with equant main-body of 2 sclerites; producing labial palps with or without a median ligula. Labial palps mucronate or stubby; 1- to 3-segmented; short in length. Glossae absent or infrequently present and penicillate or setate; paraglossae absent. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. Three diagnostic characters define the Rhynchophorate Class. First is the unique construction of the basicranium and snout. The basicranium consists of fused sclerites with few sutures; the frons and occiput are not defined. The snout is similarly distinctive, formed from the anterior prolongation of the genae, the "pregula," and the clypeal-vertical sclerite. Secondly, the mandibles are unique, with anatomically dorsal and ventral condyles swinging on a dorsal and ventral ball-and-socket articulations. The mandibles are somewhat disk-shaped and bear sharp teeth for boring or shearing resistant substrates. Lastly, the antennae is characteristically inserted on the snout.

Diversity and Natural History. The Rhynchophorate Class comprises a significant part of the taxonomic diversity of extant insects. Approximately 6.8% of all species belong to rhynchophorates (Appendix D) and the class is overwhelmingly dominated by the single family, Curculionidae (weevils). Rhynchophorates consist of 11 families, approximately 5,500 genera and approximately 60,000 species (Appendix D), corresponding to a rank-order of 8 among 34 mouthpart classes (Table 5, Fig. 131).

Rhynchophorates are an important terrestrial group of dominately obligate herbivores specializing on various plant organs (Fig. 53), often with host monospecificity (Arnett 1964, Crowson 1981). They feed on flower tissue and pollen ("mess-and-soil" pollinators) and are important agents of pollination for angiosperms with the cantharophilous pollination syndrome (Faegri and Van der Pijl 1980). They are important, often dominant consumers of plants in most terrestrial communities such as sandy substrate successional communities in England (Brown and Hyman 1986), and have strong representation in many widespread plants such as native thistles (Goeden and Ricker 1987) and *Baccharis* (Palmer 1987) of the American Southwest. Rhynchophorates are also important in the pollination of archaic angiosperms and cycads (Szent-Iveny et al. 1956, Pelmyr and Thien 1986, Norstog et al. 1986, Norstog 1987). Additionally, many rhynchophorates feed on fungi, submerged aquatic plants (Crowson 1981), indurated foodstuffs such as seeds, bark and roots (Johnson and Lyon 1976, Davidson and Lyon 1987), and the females of many species bore into wood for oviposition (Proctor and Yeo 1973).

Structural Themes. Rhynchophorates exhibit four major structural themes, indicated by the subclustering pattern of Fig. 54. Fourteen characters are primarily responsible for the division of rhynchophorate mouthparts into these four themes. Four of these characters are labral features that separate *Cimberis atteleboides* from all other curculionoid taxa. The other ten characters are dominately head-associated characters, namely head shape, rostrum/proboscis development, genal region/ malar space development, gula/hypostome development and condition of the

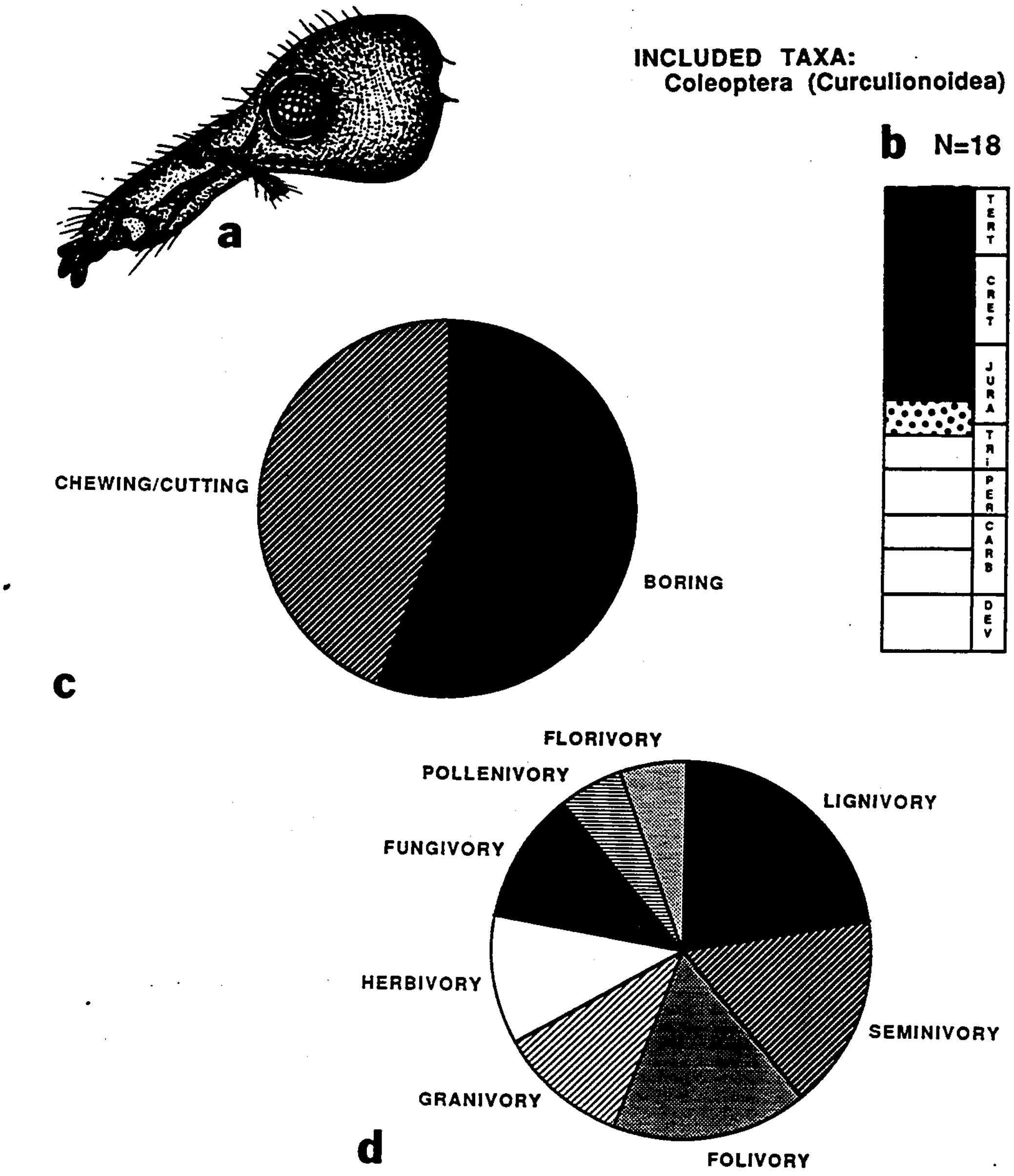


FIGURE 53. Overview of the Rhynchophorate Mouthpart Class. a, *Rhynchites auratus* Scopoli (Coleoptera: Attelabidae, data-set no. 724), after Brack-Egg (1973); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

frontal/vertical region. Other discriminating characters are food pump type, epipharynx structure, mandibular type, galeal modification and lacinial modification.

Subcluster 1 consists of the nemonychid *C. attleboides* (data-set no. 715), which retains some of the mouthpart features typical of noncurculioinoid coleopterans. Subcluster 2 comparises a relatively diverse suite of 11 oxycorynid, attelabid, brentid, apionid and curculionid taxa (bracked by data-set nos. 720 to 725 on Fig. 54). These taxa are characterized by long snouts with terminal, ratchet-shaped and swivel-articulating mandibles operated by long rope muscles originating from the head capsule proper. These forms tend to ingest indurated foodstuffs such as seeds, grain or roots, but are rarely wood-borers. By contrast Subcluster 3 consists of short- to blunt-snouted curculionids that are members of the subfamilies Scolytinae and Platypodinae. These forms occur mostly as wood-borers of gymnospermous and angiospermous trees. Finally, Subcluster 4 consists only of the belid *Dicordylus binotatus*, a rather plesiomorphic curculionid that occurs on gymnosperms and may be related to taxa describe from the Jurassic and Cretaceous (*vide supra*).

Geochronological History. Within the Coleoptera, it is generally believed that curculionoids are the most derived and recently evolved suprafamilial group (Handlirsch 1906, 1912, Gillott 1980, Crowson 1981). The oldest known, demonstrable rhynchophorates are *Archaeorrhynchus tenuicornis* Martynov and *Eobelus longipes* Arnoldi from the Upper Jurassic of Soviet Central Asia [60] (Martynov 1926, Ponomarenko 1980,

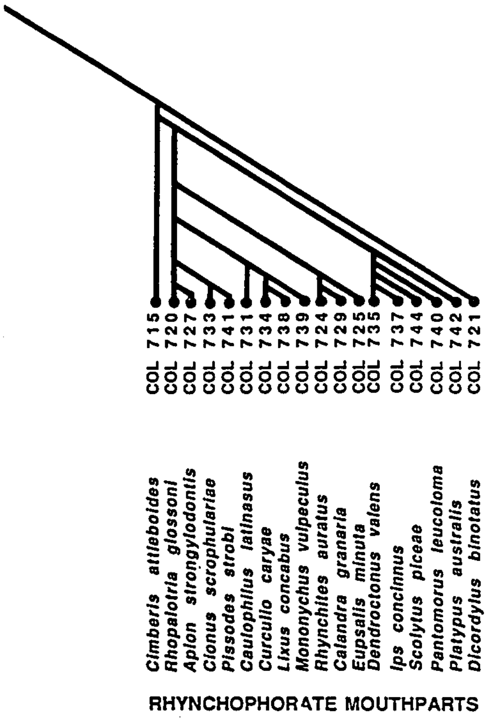

COL 715 Cimberis attleboides
COL 720 Rhopalotria glossoni
COL 727 Apion strongylodontis
COL 733 Cionus scrophulariae
COL 741 Pissodes strobi
COL 731 Caulophilus latinasus
COL 734 Curculio caryae
COL 738 Lixus concabus
COL 739 Mononychus vulpeculus
COL 724 Rhynchites auratus
COL 729 Calandra granaria
COL 725 Eupsalis minuta
COL 735 Dendroctonus valens
COL 737 Ips concinnus
COL 744 Scolytus piceae
COL 740 Pantomorus leucoloma
COL 742 Platypus australis
COL 721 Dicordylus binotatus
RHYNCHOPHORATE MOUTHPARTS

FIGURE 54. Cluster analysis dendrogram of taxa comprising the Rhynchophorate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

Hennig 1981, Crowson 1981) (Fig. 55). These forms possess the typical beak and other features of several extant, less derived families (Crowson 1976, 1981; Arnoldi et al. 1977) and are placed in an extinct family, the Eobelidae. Arnoldi et al. (1977) claim that the weevils of this deposit are the most diverse component of the beetle fauna. From a slightly younger Lower Cretaceous [56] insect fauna at Lérida, Spain, are described two weevils, one an eobelid and the other of uncertain familial affinities (Whalley and Jarzembowsky 1985, Pallerola 1986). The occurrence of a weevil from Lower to Upper Cretaceous deposits from South Dakota [50] is documented by Northrup (1928), who placed the fossil, *Curculionites*, in the Curculionidae. It resembles extant genera that are associated with conifer needles. Wood-boring adult curculionids occur in the Eocene London Clay fauna near Bognor Regis, England [26] (Britton 1960, Venables and Taylor 1962), as well as other mid-Tertiary deposits [9,3] (Heer 1847, Zeuner 1938). Rhynchophorates from the Baltic amber fauna [19] are diverse, numerous and appear to have been partitioning numerous food resources (Larsson 1978).

An alternative approach in assessing the presence of rhynchophorates in the fossil record is the documentation of characteristic borings in fossil woods. The earliest documentation of this trace-fossil type comes from Pennsylvanian strata and consists of coprolites and oftentimes preserved frass material occurring in galleries or borings within permineralized wood fragments or "woody" stems. Wood-borings of Pennsylvanian-age [coeval with 96] occur in the wood of the cordaitalean gymnosperm *Premnoxylon* (Cichan and Taylor 1982, Labandeira

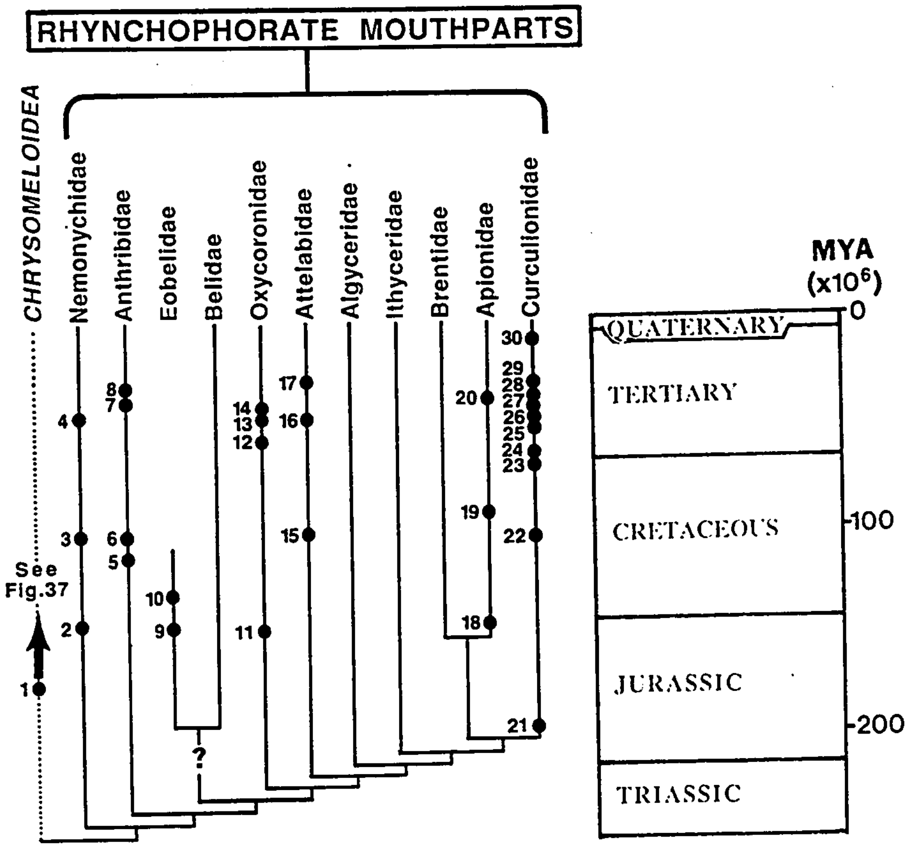


FIGURE 55. Geochronologic history of the Rhynchophorate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Morimoto (1962), Vanin (1976), Sanborne (1981), Crowson (1981) and Lawrence and Newton (1982). The taxonomic level of analysis is the family. The outgroup is Chrysomeloidea. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

and Beall 1990), the stem of the pteridophyte *Psaronius* (Rothwell and Scott 1983; Labandeira and Beall 1990), the stem of the calamites *Sigillaria* (Geinitz 1855), the trunk outer cortex of the lycopod *Lepidodendron* (Friese and Gothan 1952) and "*Cardiocarpon*" wood (Williamson 1880)--all from coal-associated deposits of the midwestern United states and western Europe. Although insects are implicated as the wood-boring agents (Geinitz 1855, Scott and Taylor 1983), no definitive evidence indicates presence of rhynchophorates during Pennsylvanian times. However, by Triassic and Jurassic times, bored coniferous wood includes structures referred to buprested larvae, anobiid adults, and *Scolytus*-like and *Ips*-like curculionids ([68], Jurasky 1932). Other documented wood borings have been described by Walker (1938) for bored *Araucarioxylon* from the Chinle Formation of the Petrified Forest of Arizona [77] and Linck by (1949) for similar bored wood of the Keuper Series of Germany. Although additional examples occur for the Cretaceous Period (e.g. [57], Blair 1943), it is during the Tertiary when the first good examples of wood bored by rhynchophorates occur (Brues 1936; Crowson 1976, 1981). In summary, although bored Pennsylvanian woods indicate the probable presence of xylophagous insects, the first suggestive trace-fossil evidence for rhynchophorates originates from Triassic coniferous woods, significantly prior to first rhynchophorate body-fossil in the Upper Jurassic.

Previous Designations. The term "Rhynchophora" was used as a formal taxonomic term by many entomologists (e.g. Handlirsch 1906-1908, Ting 1936, Comstock 1940) to refer to weevils, although it has been recently supplanted by the synonym, Curculionoidea (e.g. Richards and Davies 1977, Crowson 1981). Because of its present disuse as a formal taxonomic name, its long previous history as a referent to a highly stereotyped group of beetles (weevils) and its etymology from the Greek, meaning "snout," I am using the term **rhynchophorate** to define this distinctive mouthpart class. Previous references to forms now occurring in the Rhynchophorate Class have been considered under the more general designation, mandibulate, or some variant thereof. Chaudonneret (1983) considered the cranial and mouthpart modifications of weevils as one consequence of rostrum formation in generalized mandibulate insects. The other major group of rostrum-bearing mandibulate insects, mecopterans, was listed as a separate modification of the "*consequence de la formation d'un rostre chez les insectes broyeurs*."

Review of Literature. Major compilations of rhynchophorate mouthparts and head capsules include Stickney (1923, head capsules only), Ting (1933, mouthparts only), Williams (1938, maxillae and labia only) and Morimoto (1962, all structures). Species-based accounts include Muñiz and Barrera (1969) for the oxycorynid *Rhopalotria glossoni* Schaeffer, Brack-Egg (1973) for the attelabid *Rhynchites* Scopoli, Dennell (1942) for the curculionid *Calandra granaria* Linneaus, Donges (1954) for the curculionid *Cionus scrophulariae* Linneaus and McClenahan (1904) for the curculionid *Nononychus vulpeculus* Fabricius.

8.3.11. Pectinate Class
(Class 10)

Description. Head spheroidal to dorsoventrally flattened; nonproboscate (mandibular tusks in some); nonretractile. Prothoracic legs often part of feeding apparatus. Gena minimally to prominently developed; gular region absent. Antennae setaceous; ocelli 3; compound eyes moderately developed and dichoptic. Mouthparts mandibulate, hypognathous, nonretractile, consisting of single element asymmetry. Food pump variously developed.

Clypeus quadrate to transversely elongate; undivided. Labrum quadrate to transversely elongate; undivided; margin commonly pectinate, often notched medially. Hypopharynx trilobed, with rows of setae or bristles on superlingulae; epipharynx mostly setate, less commonly membranous or spatulate. Mandibles dicondylic; distally expanded; pectinate (diatom rakes, prosthecae), or caniniform; musculation of abduction/adduction. Maxillae with main-body of 1 or 2 sclerites; stipes squarose to elongate-rectangular; bearing a fused galeae and laciniae (mala) and palpi. Maxillary palp penicillate; 3- or less often 2-segmented; intermediate to long in length. Galea and lacinia fused into a mala with pectinate bristles mesially and a raker distally. Labium with an elongated main-body undivided or divided into 2 sclerites; bearing glossae, paraglossae and palpi. Labial palpi pectinate or penicillate; 3- to less commonly 2-segmented; intermediate in length. Glossae setate or less commonly lingulate; paraglossae penicillate or less often a broadly attached lobe. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. A dominant feature of the Pectinate Mouthpart Class is the pervasive presence of pectinate, or less commonly, brustiate mouthparts, including palps and lobes. The most distinctive feature is a distally-expanded (securiform) mandible with two articulating points and a third sliding contact point with the cranium. The mandibular dentition is characteristically provided with a row of acuminate incisors, an articulating brustiate prostheca, and a distinct molar region consisting of a pectine on one mandible and a more typical grinding surface on the opposite mandible. The hypopharynx has a unique, large, superlingulal lobes. Paraglossae are broad and transversely-elongated.

Diversity and Natural History. The Pectinate Mouthpart Class comprises the aquatic stages of ephemeropterans, which feed predominately by collecting-filtering, with some deposit-feeding and scraping, mostly on plant and animal detritus and algae (Cummins and Klug 1979, Edmunds 1984) (Fig. 56). Live vascular tissue is rarely used. Pectinates exhibit minimal dietary specificity and consume a wide variety and size range of organic detritus, including recycled faecal matter (Mattingly 1987b). A few species are predators, especially during the later naiad stages. The life-habits of members of this class include clinging to hard substrates, subordinately burrowing and sprawling on submerged leaves of vascular hydrophytes, and swimming that alternates with longer periods of clinging or sprawling (Needham, Traver and Hsu 1935; Cummins and Merritt 1984; Edmunds 1984). Together with members of the Mouthbrush (Sect. 5.9) and Mandibulobrustiate (Sect. 5.10) mouthpart

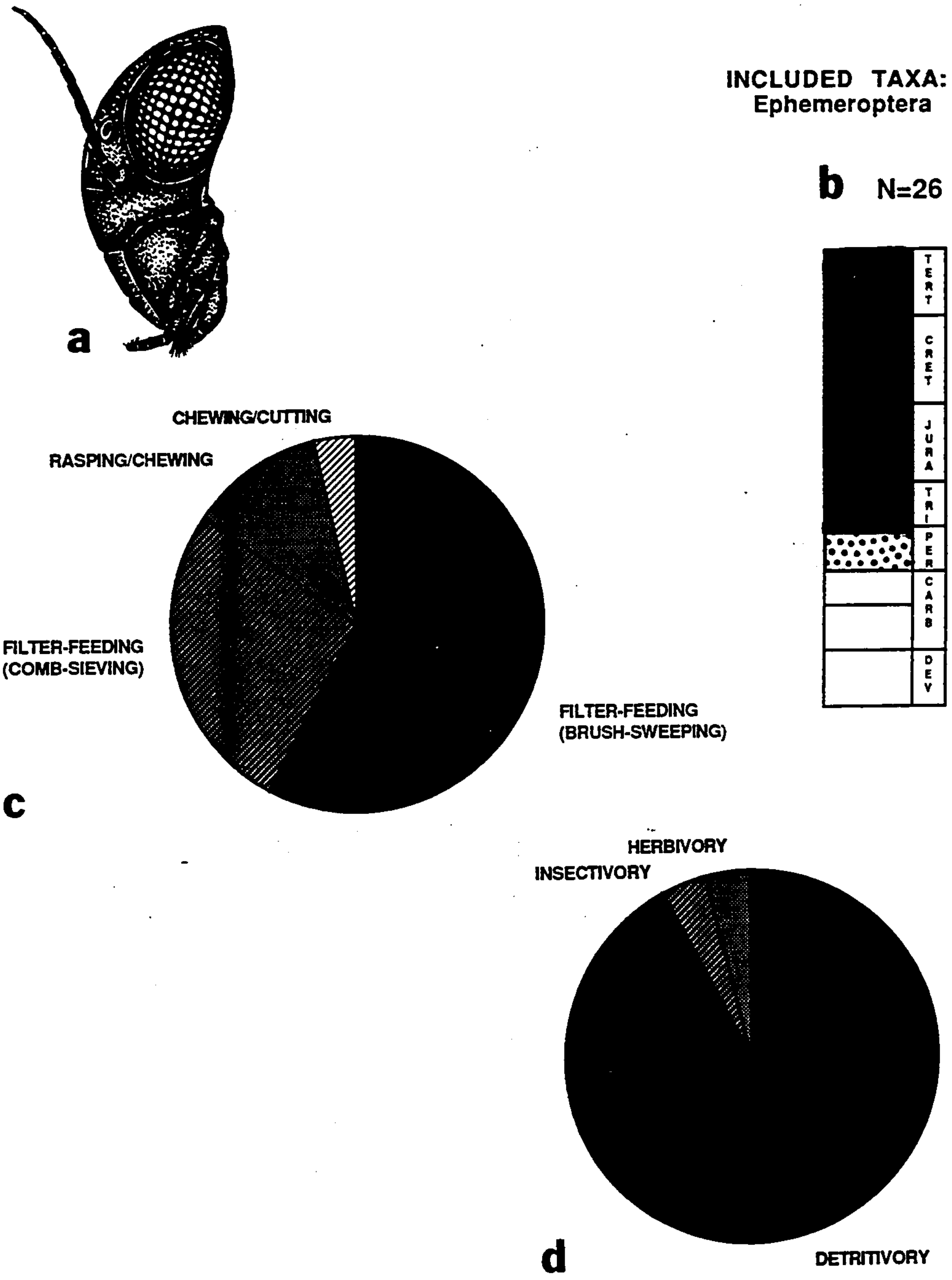


FIGURE 56. Overview of the Pectinate Mouthpart Class. a, *Siphlonurus aestivalis* Eaton (Ephemeroptera: Siphlonuridae, data-set no. 25), after Schönmann 1981; b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

classes, members of the Pectinate Class are the principal primary consumers in lentic and lotic freshwater ecosystems (Cummins and Klug 1979, Merritt and Wallace 1981).

Pectinates are a relatively depauperate group in terms of taxonomic diversity. The Pectinate class incorporates 18 families, about 230 genera and about 2200 species, amounting to 0.24% of all insects (Appendix D). This corresponds to a rank-order of 24 out of 34 mouthpart classes (Table 5, Fig. 131). Although this represents an insignificant percentage in terms of overall insect diversity, it belies their abundance and prominent trophic role in freshwater habitats.

Structural Themes. Pectinate mouthparts are categorizable into four subclusters, or themes (Fig. 57). Approximately 11 characters, distributed among most of the head and mouthpart regions, resolve pectinate mouthparts into these four major groups. The discriminating characters are genal region/malar space development, feeding-related modifications, mouthpart placement, food pump type, hypopharynx type, epipharynx type, mandible type, mandibular dentition, type of maxillary appendages, galeal modifications and paraglossal modifications. These characters taxonomically partition ephemeropteran naiads into the four subclusters mentioned above along superfamilial lines.

Subcluster 1 comprises the siphlonurid *Ameletus inopinauts* and the oligoneurid *Isonychia ignota* (data-set nos. 24 and 30 of Fig. 57) and represents the most pronounced divergence within pectinates. These taxa are members of the superfamily Baetoidea. Subcluser 2 is the most taxonomically diverse assemblage, consisting of members of the

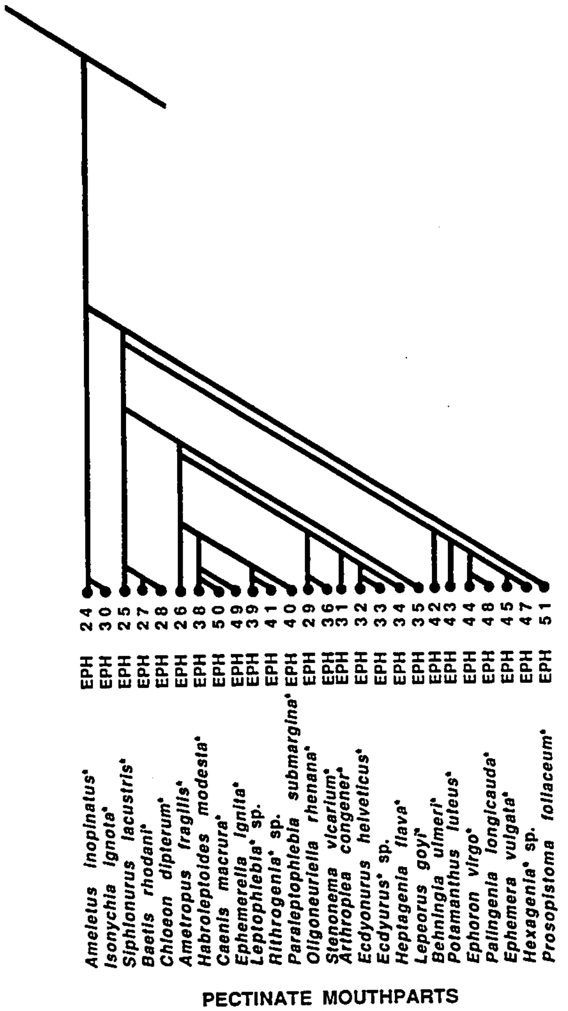

EPH 24 Ameletus inopinatus*
EPH 30 Isonychia ignota*
EPH 25 Siphlonurus lacustris*
EPH 27 Baetis rhodani*
EPH 28 Chloeon dipterum*
EPH 26 Ametropus fragilis*
EPH 38 Habroleptoides modesta*
EPH 50 Caenis macrura*
EPH 49 Ephemerella ignita*
EPH 39 Leptophlebia* sp.
EPH 41 Rithrogenia* sp.
EPH 40 Paraleptophlebia submargina*
EPH 29 Oligoneuriella rhenana*
EPH 36 Stenonema vicarium*
EPH 31 Arthroplea congener*
EPH 32 Ecdyonurus helveticus*
EPH 33 Ecdyurus* sp.
EPH 34 Heptagenia flava*
EPH 35 Lepeorus goyi*
EPH 42 Behningia ulmeri*
EPH 43 Potamanthus luteus*
EPH 44 Ephoron virgo*
EPH 48 Palingenia longicauda*
EPH 45 Ephemera vulgata*
EPH 47 Hexagenia* sp.
EPH 51 Prosopistoma foliaceum*
PECTINATE MOUTHPARTS

FIGURE 57. Cluster analysis dendrogram of taxa comprising the Pectinate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

superfamilies Baetoidea, Leptophlebioidea, Ephemerelloidea and Caenoidea (bracketed by data-set nos. 26 to 35 in Fig. 57). This group is dominately epibenthic in habit and is characterized by equant, pectinate and prosthecate mandibles. By contrast, Subcluster 3 is comprised of members of the Superfamily Ephemeroidea, which are burrowing forms bearing mandibles with long, falcate tusks as mandibular extensions. Lastly, Subcluster 4 consists of the structurally divergent prosopistomatoid, *Prosopistoma foliaceum*.

Geochronologic History. Controversy exists as to whether aquatic nymphs (naiads) are a primitive character within the Paleoptera (Hutchinson 1981, Messner 1988) and thus whether pectinate mouthparts are a primitive or derived condition in ephemeropterans. All major cladistic treatments of insects indicate that the Ephemeroptera and Odonata are the sister group (or groups) of all other winged insects (Kristensen 1975, 1981; Hennig 1981; Boudreaux 1987) and thus have a long ancestry. This evidence and the presence of Carboniferous fossils referrable to adult ephemeropterans or its stem-group (e.g.Carpenter 1963) suggest that ephemeropterans were in existence during the Late Carboniferous. However, for the purposes of documenting the history of the Pectinate mouthpart class, this conclusion must be tempered by the absence of Carboniferous ephemeropteran nymphs.

The oldest ephemeropteran, *Bojophlebia prokopi* Kukalová-Peck 1985, is known from giant adult and nymphal specimens occurring in Late Carboniferous tuffites from Czechoslovakia [98] (Fig. 58). Nymphs of this species have been figured and described by Kukalová-Peck (1983,

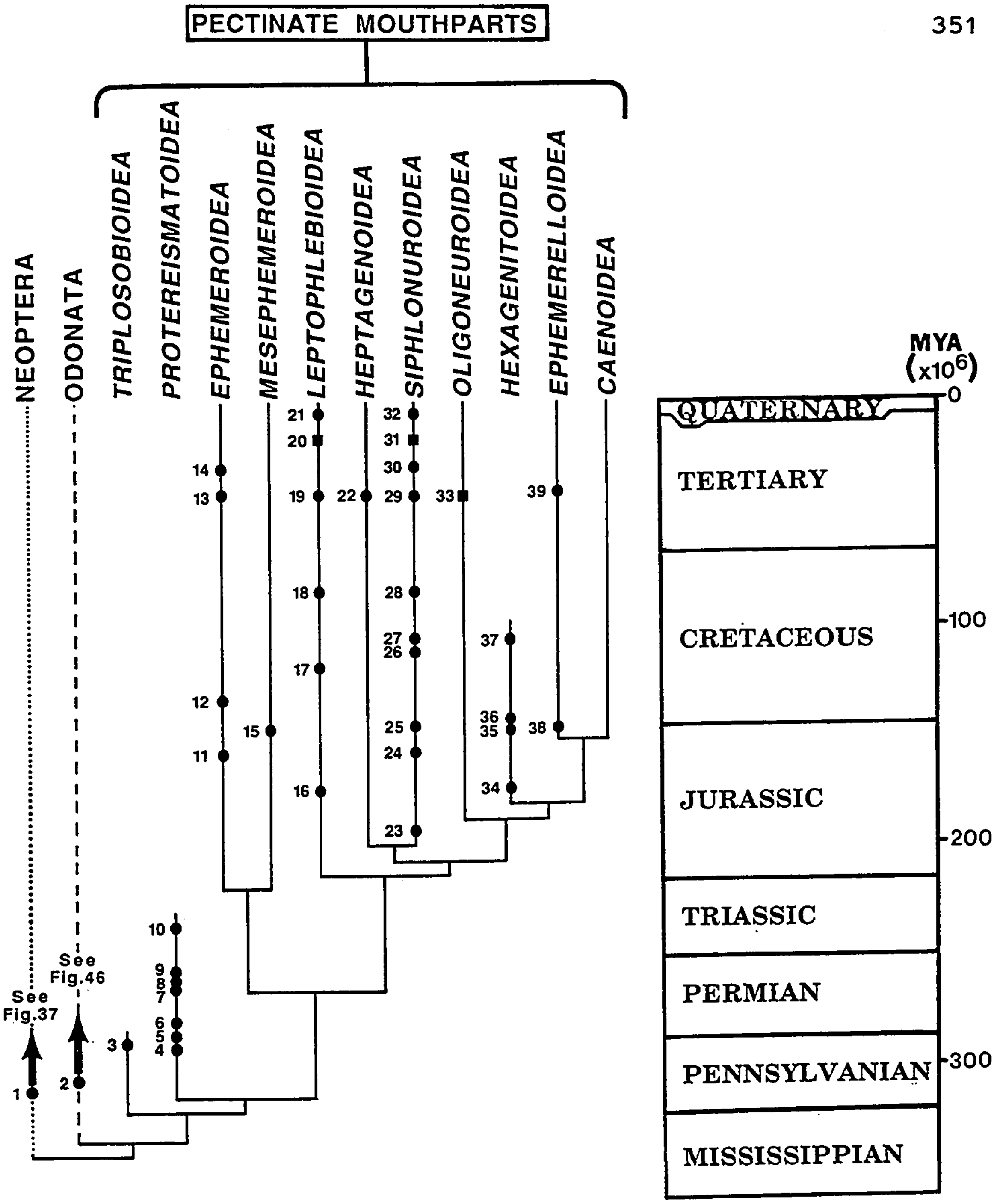


FIGURE 58. Geochronologic history of the Pectinate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Chernova (1980) and Hennig (1981). The taxonomic level of analysis is the superfamily. The outgroup is Odonata; the relationship of Neoptera to Odonata + Ephemeroptera is also indicated. These fossil occurences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

1985) and possessed gill-like abdominal structures. If these structures are indeed aquatic respiratory organs, then this specimen is probably the earliest known aquatic nymph. Nevertheless, this fossil and two other ephemeropteran nymphs described from Mazon Creek deposits [97] (Kukalová-Peck 1985) do not represent the earliest occurrences of the Pectinate Mouthpart Class since they have heads with prominent, bulging eyes and prognathous "mouthparts [that] are well-developed, sclerotized and adapted for general feeding" (Kukalová-Peck 1985: 943) and were probably predaceous in life-habits. The Pectinate Mouthpart Class consequently is probably a post-Pennsylvanian and possibly a post-Paleozoic development. Thus, in this case, common membership in the same order as modern mayflies does not guarantee concomitant membership in the same nymphal mouthpart class.

The next oldest known identifiable ephemeropteran is *Triplosoba pulchella* (Brongniart) 1893, an adult from the Upper Carboniferous of the Commentry Shale of France [95] (Demoulin 1956a, Carpenter 1963, Chernova 1970). This specimen is placed in the suborder Protephemeroptera of the order Ephemeroptera (Chernova 1970) or as a member of the stem-group of the Ephemeroptera (Hennig 1981). Several adults have been documented from the Lower Permian of Kansas [90], the Lower Permian of Cherkarda in the USSR [89], the Upper Permian at Tikhie Gory in the USSR [88] and the lowermost Permian of the lower Rothliegende Series of Germany [94]. These deposits have yielded adult ephemeropteran compression fossils of the suborder Permoplectoptera, including *Protereisma* of the monotypic Protereismatidae, *Misthodotes* of the monotypic

Misthodotidae and *Doter* of the monotypic Eudoteridae (Sellards 1907; Tillyard 1932, 1936; Carpenter 1933; Chernova 1965, 1970; Kinzelbach 1970; Kinzelbach and Lutz 1984). Adult permoplectopterous forms are additionally described from Upper Permian deposits of Eurasia [86] (Martynov 1932). Hennig (1981) considers the Permoplectoptera to be a member of the stem-group of the Ephemeroptera and not true ephemeropterans.

Permoplectopterous nymphs from the Early Permian [92, 90,89] have been described and discussed by Chernova (1965), Demoulin (1966, 1970) and Kukalová (1968). Although some difficulties exist in associating aquatic nymphal stages with adult stages in the same deposit, wing venation is frequently used as a diagnostic character (Kukalová 1968). The association of protereismatid nymphs and adults was demonstrated by Kukalová's (1968) study of Lower Permian nymphs from Kansas [90] and from the Boskovice Furrow of Czechoslovakia [92]. These nymphs possessed typical aquatic specializations of extant ephemeropterans, but because of the presence of robust, incisiform mandibles in one specimen, Kukalova (1968) indicated that they were predaceous, unlike most modern forms. A somewhat younger specimen, the heptagenoid nymph, *Mesoplectopteron longipes* Handlirsch 1918, has been described from the Lower Triassic Bunter Sandstone of France [81] (Hennig 1981). This specimen is undoubtedly a member of the Pectinate class and, in the absence of further details on the mouthparts of Paleozoic forms, is considered the earliest known member of the Pectinate Mouthpart Class.

Jurassic members of the Pectinate mouthpart class are more abundant. A leptophlebiid nymph, *Mesobaetis sibirica* Brauer, Redtenbacher and Ganglbauer 1889, has been described from the Lower Jurassic of Lake Baikal, USSR [67] (Hennig 1981, but see Hubbard and Savage 1981) and from Middle Jurassic deposits of northeastern China [64] (Hong 1983). From the same two deposits is recorded the leptophlebiid nymph, *Mesoneta antiqua* Brauer, Redtenbacher and Ganglbauer 1889 (Chernova 1969, 1971; Hubbard and Savage 1981). From the Upper Jurassic of Transbaikalia, USSR [62] and the coeval Ondai Sair Formation of Mongolia, adults and nymphs of the giant *Ephemeropsis* have been found (Demoulin 1954a, 1956b, Chernova 1961; and Cockerell 1925, 1927; respectively). This form has been placed in the extinct family Hexagenitidae (Demoulin 1953), and there is a suggestion that it may have oligoneurid or siphloneurid affinities (Chernova 1961, Hennig 1981). From the same deposit in the USSR, Chernova (1977) has documented the first occurrence of nymphs belonging to the modern families Paligeniidae and Behingiidae. By contrast, Upper Jurassic strata of Germany [61] bear adult members of the extinct families Mesephemeridae (Carpenter 1932), Paedephemeridae (Lameére 1917) and Hexagenitidae (Lameére 1917, Demoulin 1967).

The Cretaceous, by contrast, marks the beginning of documented occurrences of many modern families. The lowermost Cretaceous of Spain [56] has produced the palengeniid *Mesopalingea lerida* Whalley and Jarzembowski 1985, whose mandibles were described as follows:

> Nymph with broad, flat, mandibular tusks with inward pointing apical tooth on each tusk. Outer margin of tusk with irregular edge formed by setal sockets. Each tusk has large setal bases indicating that there

> were strong setae (not preserved). Long curved mandibles have double molar surface. (pp.384-385).

In slightly younger Lower Cretaceous deposits southern Australia [53], at least three relatively well-preserved genera of siphlonurid nymphs are preserved, with details of the mouthparts and head evident (Jell and Duncan 1986). As for the Paleogene, the deposit most diverse in members with pectinate mouthparts is Lower Oligocene Baltic amber [19] of northern Europe, containing eight families and 26 genera of mayflies (Demoulin 1965, 1968; Larsson 1978).

Previous Designations. Members of the Pectinate Class, namely ephemeropteran naids, have been alluded to in previous mouthpart classifications. In 1962 Metcalf et al. defined the category as "chewing type: brushing, spatulate or scraping subtype," which accurately describes some ephemeropteran naiads. Later references include the "filtering type" of Ross et al. (1982) and "filter-feeding" of Smith (1985)--feeding types that definitely include members of the Pectinate Class (Table 6). While the term **pectinate** has not been applied to ephemeropteran naiads as a mouthpart group, I am using the term as a name for the class because of the ubiquity of coarsely-arranged, unclumped setae used for filtering and other forms of detritus collection.

Review of Literature. General references for mouthpart and head structure of North American forms include Morgan (1913), Murphy (1922), Spieth (1933a, 1933b) and Edmunds (1984). Needham, Traver and Hsu (1935) presented an ecological and functional account of mayfly structure. Sternfeld (1907) described the mouthparts of several northern European species.

Monographic accounts of pectinate species are provided by Schonmann (1981) for the siphlonurid *Siphlonurus aestivalis* Eaton, Brown (1961) for the baetids *Baetis rhodani* Pictet and *Chloeon dipterum* Linneaus, Froehlich (1964) for the heptageniid *Arthroplea congener* Bengtsson, Strenger (1954) for the heptageniid *Ecdyonurus helveticus*, Schonmann (1981) for the heptageniid *Lepeorus goyi* Peters and Strenger (1954) for the leptophlebiid *Rithrogenia hybrida*. Vassal (1947) and Noars (1961) have discussed details of the hypopharyngeal structure. Hardland-Rowe (1953) has presented a short account of the use of silk nets in the feeding mechanism of a burrowing species. Analyses and summaries of flow-pattern and particle capture in ephemeropteran filter-feeding have been done by Wallace and O'Hop (1979), Wallace and Merritt (1980) and Braimah (1987a, 1987b).

8.3.12. Mouthbrush Class
(Class 11)

Description. Head spheroidal; nonproboscate; generally protractile. Genae extending dorsoventrally, comprising most of cranium and delimiting frontovertical region; gula prominent, rarely minimally developed. Antennae setigerous, less often palpiform or stubby; stemmata (ocelli) two, commonly more than 3; compound eyes absent or moderately developed in some. Mouthparts mandibulate, prognathous, symmetrical and nonprotractile. Food pump clypeal or pharyngeal.

Clypeus variously shaped; fused to frons; often not evident. Labrum vertically elongate, rarely otherwise; undivided; margin pectinate, penicillate (labral fan) or rarely straight to curvilinear.

Pharyngeal region well developed; hypopharynx a sclerotized molar structure with teeth, a lingulate lobe, or pectinate with dentate superlingulae, rarely otherwise; epipharynx penicillate, setate or denticulate/spinose, rarely otherwise. Mandibles dicondylic; mostly falcate, tetragonal or securiform; pectinate, incisiform with prominent mesial brush, or dominately incisiform; musculation of adduction/ abduction type. Maxillae with variously shaped main-body of one sclierite; bearing a fused galea and lacinia (mala) and palpi. Maxillary palpi stubby or mucronate; 1- to 2-segmented; short in length. Mala penicillate, setate/spinose, or generalized. Labium reduced, with elongate main-body of 1 or 2 sclerites, bearing a glossa or ligula only. Labial palps almost always absent. Glossa (ligula) setate, penicillate or rarely bearing silk glands. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. The Mouthbrush Class is only moderately stereotyped and converges in some structural details with the Pectinate Class (Section 8.3.11). However, there are some unique or near-exclusive features. First, the persvasiveness of brushlike or pectinate structures on virtually all mouthpart elements is noteworthy. These filtering or scraping structures also occur on projecting appendages, including antennae, labral fan stalks and maxillary palps. Secondly, the cephalic capsule is different from those of the hemimetabolous Pectinate Class: the mouthbrush head lacks typical adult sensory organelles and mouthbrush members are often blind. Thirdly, the labrum is frequently modified into large, pedunculate, lateral fans or into a marginal medial fan or pectines with long setae and spinose processes. Lastly, the labium has been transformed into a truncate, deltoid sclerite bearing serrated spines or a brush.

Diversity and Natural History. Members of the Mouthbrush Class dominantly constitute aquatic nematoceran dipteran larvae that are major detritivores and herbivores (uncommonly carnivores) in freshwater ecosystems (Fig. 59). The mouthpart class also includes the terrestrial larvae of wood-boring buprestid coleopterans and leaf-mining phyllocnistid and gracillariid lepidopterans. The class taxonomically comprises nearly all nematocerans, except for ceratopogonids, several undiverse bibionid families and cecidomyiids. The Mouthbrush Class consists of approximately 43,800 species, approximately 900 genera and 16 families (Appendix D). Its rank-order within the 34 mouthpart classes is 10 (Table 5, Fig. 131)--a significant representation of a major ecological group of holometabolous insects.

Ecological partitioning of aquatic food resources among most members of the Mouthbrush Class has been extensively documented (Wallace and Merritt 1980, Merritt and Wallace 1981, Cummins and Merritt 1984, Anderson and Cargill 1987). From discussions in Surtees (1959), Pucat (1965), Chance (1970) and Cummins and Merritt (1984), aquatic nematocerous larvae occupy three major feeding roles or functional feeding groups (Cummins 1973) in lotic and lentic habitats. These are (i) filter-feeders or collectors, (ii) browsers, grazers or scrapers and (iii) predators. Filter-feeders occur in the neuston, epibenthic and infaunal zones and consist of anopheline and many culicine mosquitoes

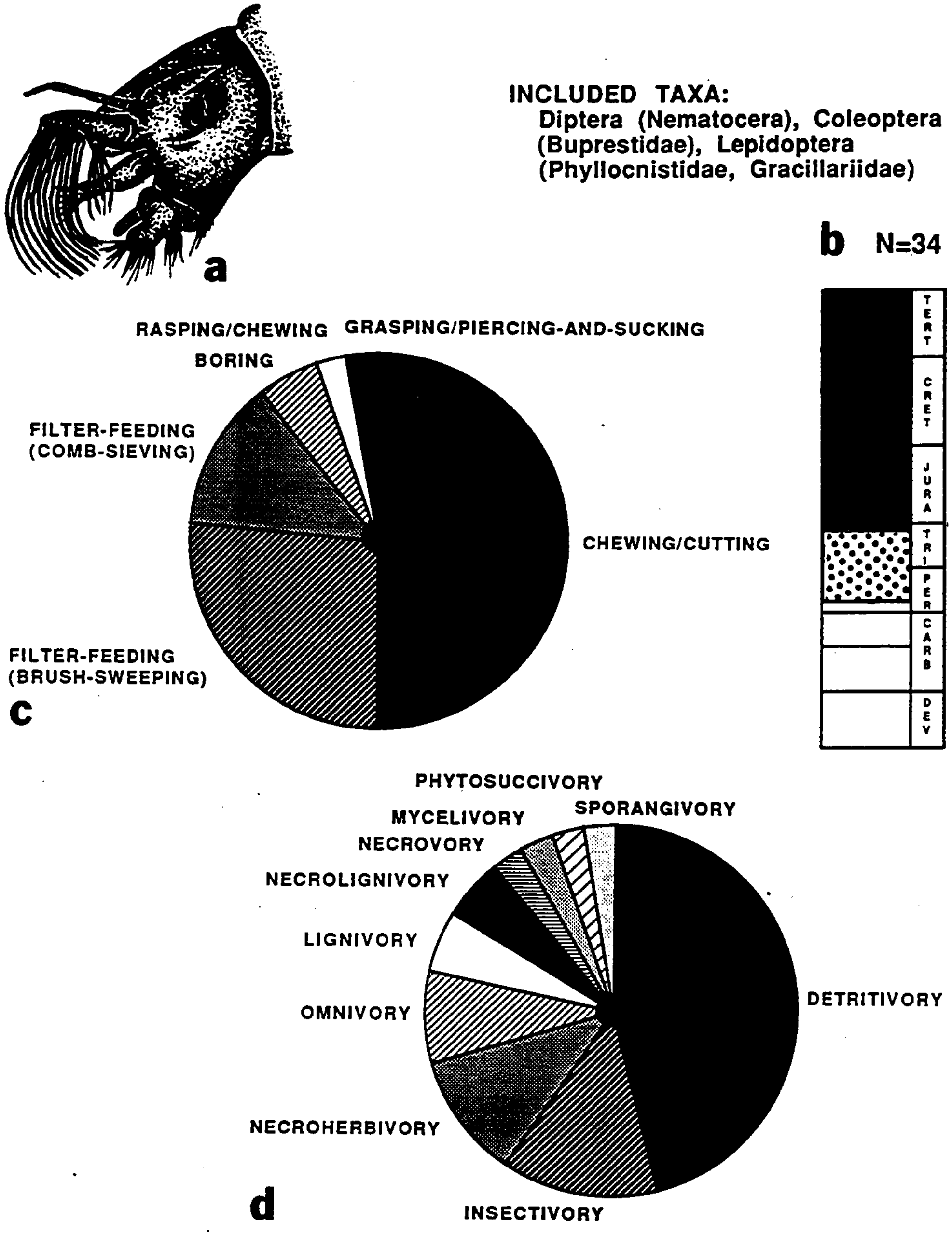


FIGURE 59. Overview of the Mouthbrush Mouthpart Class. a, *Simulium venustum** Say (Diptera: Simuliidae, data-set no. 838), after Peterson (1981); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

(Pucat 1965, Newson 1984), cephalic fan-bearing simuliids (Peterson 1984) and most chironomids (Coffman and Ferrington 1984), the latter of which often filter-feed by silken nets (Leathers 1922, Walshe 1947, Merritt and Wallace 1981). Browsers are mostly bottom-feeding and include many culicine mosquitoes (Surtees 1959, Pucat 1965), some simuliids (Chance 1970), some chironomids (Leathers 1922), tipulids (Byers 1984), ptychopterids (Mattingly 1987a), dixids and psychodids (Merritt and Schlinger 1984). Predators feed by engulfing prey and are dominately chaoborids (Pucat 1965, Sih 1987), some culicine mosquitoes (Surtees 1959) and some chironomids (Chance 1970, Coffman and Ferrington 1984). Aquatic larval dipteran forms with mouthbrushes are diverse taxonomically as well as trophically, and chironomids alone often account for at least 50% of the macroinvertebrate fauna in temperate freshwater ecosystems (Coffman and Ferrington 1984).

Buprestid larvae are vermiform, apodous, wood-boring larvae with enlarged cranial/prothoracic capsules to support massive mandible musculature for boring into wood. Buprestid larvae possess characteristic sawlike mandibles for cutting through cambial and other woods (Crowson 1981). Similarly, modifications in leaf-mining phyllocnistid and gracillariid larvae include an enlarged head to support mouthpart musculature and mandibular specializations for macerating leaf tissue. Both larval types are frequently host-specific, and frequently leaf-miners specialize on consumption of particular leaf tissues, such as the mesophyll, pallisade or vascular bundles (Needham et al. 1928, Hering 1950). Like aquatic members of the mouthbrush class, larval buprestids, phyllocnistids and gracillariids possess prominent setate mouthparts.

Structural Themes. There are four major themes that are expressed as subclusters within the dendrogram of Mouthbrush Mouthparts (Fig. 60). They are (i) a tipuloid/buprestid theme (data-set entries 537 to 800 in Fig. 60) of aquatic, semiaquatic and wood-boring larvae, (ii) a culicoid/bibionoid theme (805 to 832) of mostly aquatic or semiaquatic dipterans that form the core of the dendrogram, (iii) a small subcluster of two lepidopterans and the dipteran *Bittacomorpha clavipes* Fabricius (808 to 1123), comprising leaf-mining and semiaquatic larvae and (iv) the single, isolated taxon of *Perissosoma fusca* Colless (849), a borer in rotting wood. Although dominated by aquatic particulate feeders, the presence of leaf-miners, wood-borers and semiaquatic/semiterrestrial larvae provide an ecological depth to this mouthpart class.

The tipuloid/buprestid subcluster is differentiated from the three other groups principally by presence of palpiform antennae, an undivided and transverse clypeus, and absence of ocelli and a labral fan. Whereas the culicoid/bibionoid subcluster is dominated by culicids, chironomids and simuliids, it also includes a tanyderid (805) and a smattering of diverse bibionoid taxa such as a pachyneurid (550), an axmyiid (851), a bibionid (856), a sciarid (865) and a mycetophilid (866). Unique features of this relatively diverse subcluster include filiform or pectinate antennae, a pectinate or penicillate labral margin (often a labral fan) and glossae modified as brushes of abundantly setate pectines. These structures are involved in filter-feeding or filter-sieving in freshwater habitats. There is evident subdivision of this subcluster into distinctive chironomid/bibionoid, chaoborid/culicid and

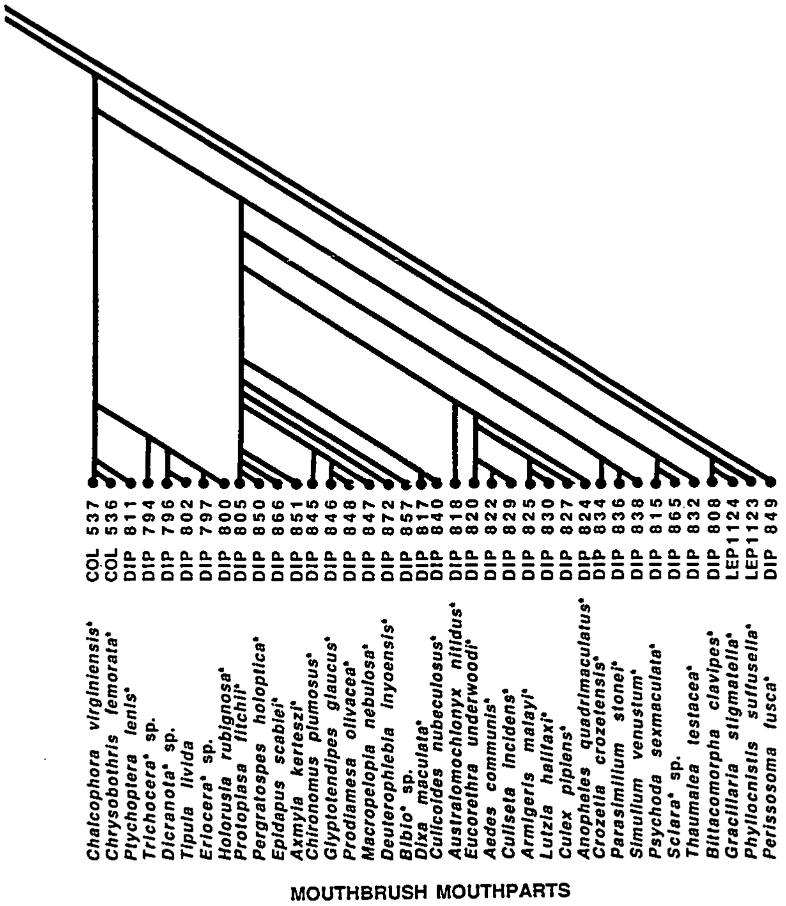

COL 537 Chalcophora virginiensis*
COL 536 Chrysobothris femorata*
DIP 811 Ptychoptera lenis*
DIP 794 Trichocera* sp.
DIP 796 Dicranota* sp.
DIP 802 Tipula livida
DIP 797 Eriocera* sp.
DIP 800 Holorusia rubignosa*
DIP 805 Protoplasa fitchii*
DIP 850 Pergratospes holoptica*
DIP 866 Epidapus scabiei*
DIP 851 Axmyia kerteszi*
DIP 845 Chironomus plumosus*
DIP 846 Glyptotendipes glaucus*
DIP 848 Prodiamesa olivacea*
DIP 847 Macropelopia nebulosa*
DIP 872 Deuterophlebia inyoensis*
DIP 857 Bibio* sp.
DIP 817 Dixa maculata*
DIP 840 Culicoides nubeculosus*
DIP 818 Australomochlonyx nitidus*
DIP 820 Eucorethra underwoodi*
DIP 822 Aedes communis*
DIP 829 Culiseta incidens*
DIP 825 Armigeris malayi*
DIP 830 Lutzia halifaxi*
DIP 827 Culex pipiens*
DIP 824 Anopheles quadrimaculatus*
DIP 834 Crozetia crozetensis*
DIP 836 Parasimulium stonei*
DIP 838 Simulium venustum*
DIP 815 Psychoda sexmaculata*
DIP 865 Sciara* sp.
DIP 832 Thaumalea testacea*
DIP 808 Bittacomorpha clavipes*
LEP1124 Gracillaria stigmatella*
LEP1123 Phyllocnistis suffusella*
DIP 849 Perissosoma fusca*
MOUTHBRUSH MOUTHPARTS

FIGURE 60. Cluster analysis dendrogram of taxa comprising the Mouthbrush Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

simuliid groupings. The third subcluster is dominated by the tineoid lepidpteran taxa *Gracillaria stigmatella* Fabricius and *Phyllocnistis suffusella* Zeller but includes the dipteran *B. clavipes*. The lepidopteran members of this subcluster is characterized by head retractability, a well-developed pharyngeal food pump and presence of a silk-producing apparatus incorporating elements of the labium, hypopharynx and labium. Although these lepidopteran taxa are leaf-miners, the inclusion of *B. clavipes* is based on mouthpart features unrelated to leaf-mining. *B. clavipes* inhabits mud that is highly saturated in water. Lastly, the position of *Perissosoma fusca* Colless is remote when compared to other members of the mouthpart class and distinguished by mouthpart-related structures for boring in damp, rotten wood (Wood 1981).

Geochronologic History. From what is known of the fragmentary Lower Mesozoic fossil insect record, the earliest assured, known dipterans are Upper Triassic (Fig. 61) and consist principally of wings in coal deposits from Issyk-Kul in Soviet central Asia [73] (Crowson et al. 1967, Rohdendorf 1974, Hennig 1981, Carpenter and Burnham 1985). Rohdendorf (1957, 1974) has described from this site 54 dipteran species, some of which are placed in the relict suborder Archidiptera (an invalid assignment according to Hennig [1981]) and most of which are considered as nematoceran relatives. Since larvae are absent from this site and there is no assignment of these fossil genera to modern families, any inference that these Upper Triassic nematoceran larvae were members of the Mouthbrush Class is tentative. Most of the

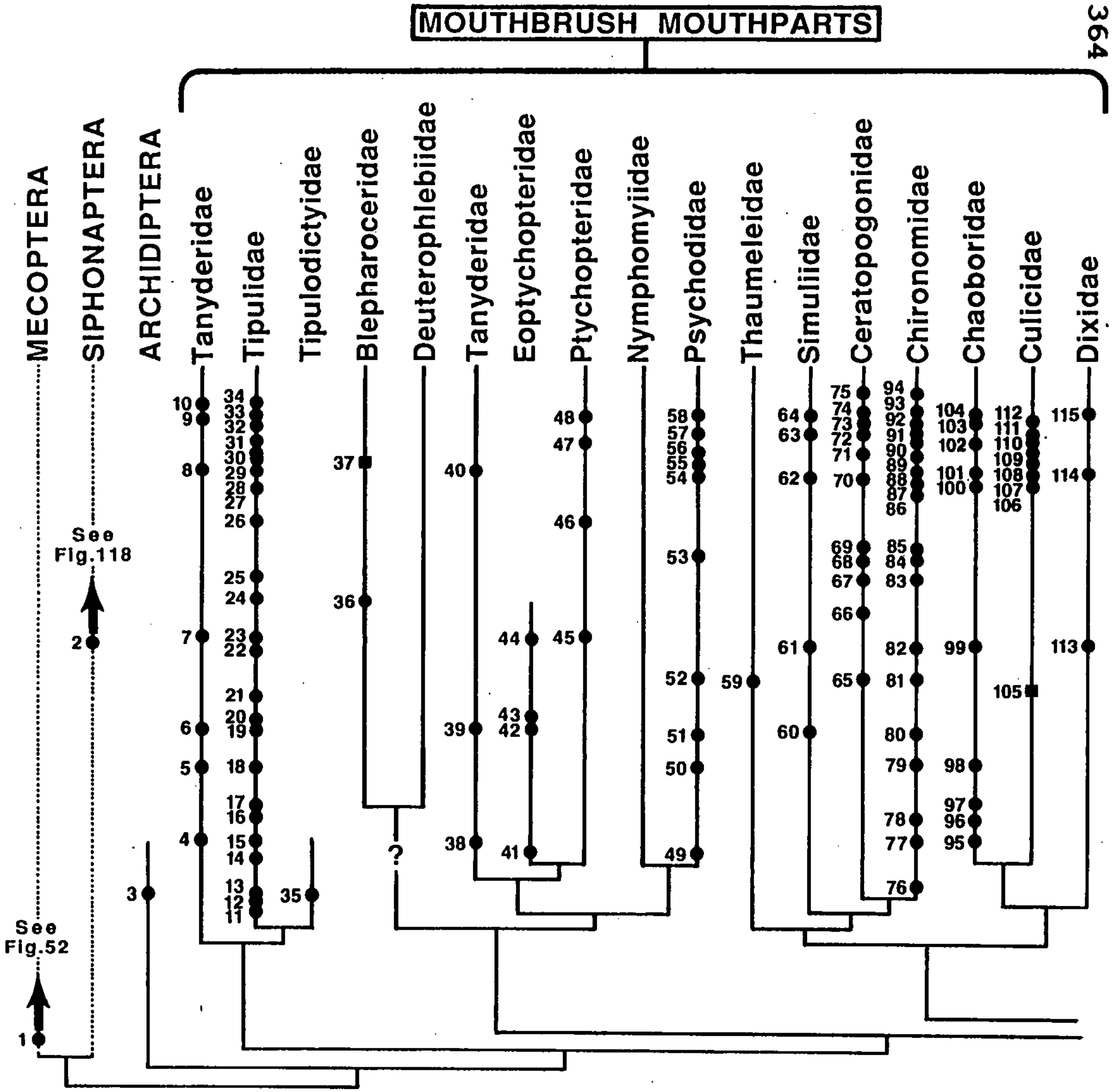
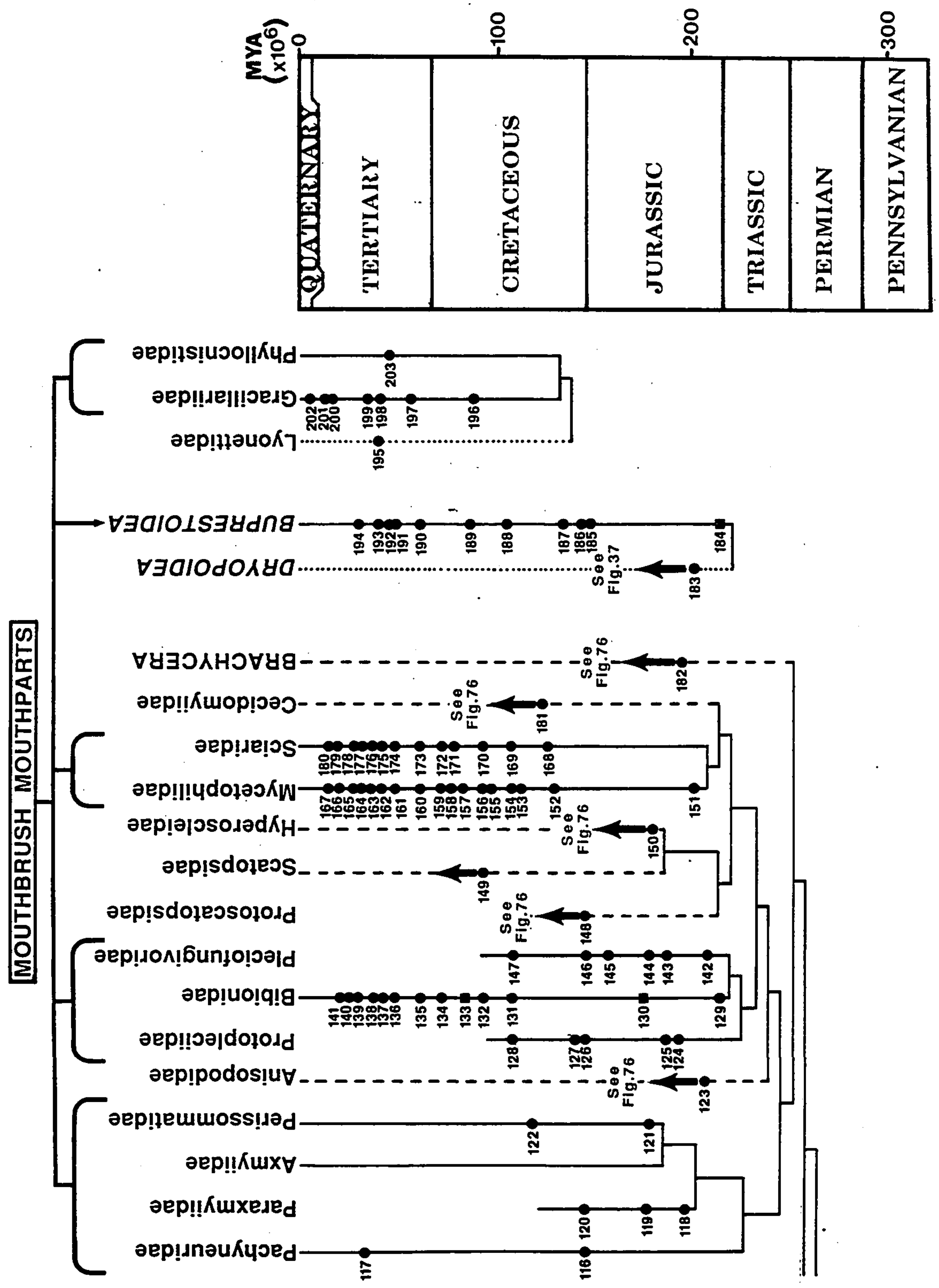


FIGURE 61. Geochronologic history of the Mouthbrush Mouthpart Class. The phylogram is continued on the next page. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Matile (1981), Rohdendorf (1974, 1980), Hennig (1981) and Jamieson (1987). The taxonomic level of analysis is the family. The outgroups are Siphonaptera + Mecoptera, Dryopoidea and Lyonettidae. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.


MYA (x10⁶)
0
100
200
300
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
PENNSYLVANIAN
MOUTHBRUSH MOUTHPARTS
Phyllocnistidae
Gracillariidae
Lyonettiidae
BUPRESTOIDEA
DRYOPOIDEA
BRACHYCERA
Cecidomyiidae
Sciaridae
Mycetophilidae
Hyperoscelidae
Scatopsidae
Protoscatopsidae
Pleciofungivoridae
Bibionidae
Protoplecidae
Anisopodidae
Perissommatidae
Axymyiidae
Paraxmyiidae
Pachyneuridae
See Fig.37
See Fig.76
117
116
118
119
120
121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203

dipterans of this fossil assemblage however have a nematoceran facies and Rohdendorf (1974: 142) claims that "Among the Upper Triassic tipulomorphs, there are undoubtedly forms related to the ancestors of other younger groups of the infraorder." Although Hennig (1981) by contrast maintains that some of these forms are unassignable to various nematoceran stem groups, he asserts that *Architendipes tschernovskyi* Rohdendorf and *Palaeotendipes alexii* Rohdendorf are assured chironomids (p.430) and *Architipula radiata* Rohdendorf is a tipulomorph (p.426). Based on these qualifications and the near exclusive presence of larvae with mouthbrushes in chironomids and tipulomorphs, I am considering the earliest documented occurrence of the Mouthbrush Class as Late Triassic. (See Fig. 61 and phylogenetic trees and cladograms of Rohdendorf [1946: 84; 1980: 113], Hennig [1981: 423], Resh [1984: 68] and Wood and Borkent [1989] for opinions regarding the timing of origin of major nematoceran groups.)

Jurassic deposits have also yielded nemoatoceran wings, including a tentative mycetophilid wing from the Lower Jurassic of England [69] (Whalley 1985). Tillyard (1933) has described architipulids from coeval sediments of the Lower Jurassic of England, and architipulids and other presumed nematocerans occur in similar age deposits from Mecklenburg, Germany [68] (Handlirsch 1908: 487-492). Additionally, a psychodid, *Mesopsychoda dasyptera* Brauer, Redtenbacher and Ganglbauer, has been reported from the Lower Jurassic of Siberia [67] (Rohdendorf 1974). From the Middle Jurassic deposits of Karatau, Soviet central Asia [60], Rohdendorf (1974) has described nine tipuloids and bibionoids. From this deposit, Kalugina (1977) has documented the earliest member of the Mouthbrush Class that can be verified as a fossil, a chaoborid larva (Wootton 1988). Additionally, adult chironomid and tipulid pupae and adults are known from the Upper Jurassic of Siberia [?62] (Kalugina, in Rohdendorf and Rasnitsyn 1980). Hong (1983) has described adult nematocerans, including tipulids from Middle Jurassic deposits of northern China [64].

With the exception of amber material, Jell and Duncan (1986) have described probably the best-preserved Mesozoic dipteran larval material, including an indeterminate tipulid, the chaoborid *Chironomaptera collessi* Jell and Duncan, and an indeterminate chironomid, all from Lower Cretaceous shales of southern Australia [53]. The cephalic fan rays of the chironomid larva are quite evident (Jell and Duncan 1986). Other taxa from the same deposit includes several indeterminate forms: tipulid pupae, adults of limoniid tipulids, adults of tanyponine chironomids, adults and pupae of simuliids and the adult sciophilinid *Pseudalysiina fragmenta* Jell and Duncan. The proportionately higher representation of aquatic larval forms over terrestrial adults is a unique feature of this deposit and the diversity of nematocerans in this deposit provides evidence for a well-differentiated Mouthbrush Class by Early Cretaceous times. Upper Cretaceous amber from Canada [35] and Siberia [37] have revealed the presence of undescribed tipuloid, chironomid, bibionid, mycetophilid and sciarid nematocerans (Carpenter et al. 1934, McAlpine and Martin 1969, Kalugina 1976).

Studies of abundant Lower Tertiary amber material, particularly from the Baltic region, have documented the occurrence of almost every extant nematoceran family with mouthbrush-bearing larvae. (See Larsson [1978] for a review of Baltic Amber [19] nematocerans). Notably, culicid larvae, abundant in the modern fauna, are not convincingly documented before the Eocene (Wootton 1988).

Wood-boring and leaf-mining members of the mouthbrush mouthpart class have a poorer fossil record than their aquatic larval members. Although buprestids have a probable earliest occurrence as adult fossils in Late Triassic deposits of the US [76] (Olsen et al. 1976), they undoubtedly are present in Upper Jurassic deposits of Eurasia [61,60] (Ponomarenko 1971, Crowson 1981). Wood-borings attributable to larval buprestids may have an earlier legacy. By contrast gracillariids and phyllocnistids are more poorly known. Gracillariid leaf-mines occur on *Platanus* (Platanaceae) leaves from Late Cretaceous strata of the USSR [39] (Kozlov 1988b). A gracillariid blotch mine resembling that of modern *Phyllonoryctes* (=*Lithocolletis*) occurs on an unknown Miocene leaf (Freeman 1965, Opler 1973) and a *Phyllocnistis*-like mine on *Cedrela* (Meliaceae) was reported from the Miocene of Wyoming [28] (Hickey and Hodges 1975). Also, body-fossils of gracillariids are known from Baltic amber [19] (Kozlov 1987). These data indicate that, for the mouthbrush mouthpart class, the wood-boring habit was present by the Late Jurassic and that the leaf-mining habit extends to the Late Cretaceous (see Section 8.3.14 for documentation of these life-habits among sericterates).

Previous Designations. The unique ensemble of mouthparts possessed by nematoceran larval dipterans has been recognized for some time (e.g. Meinert 1886). The nomenclature for referring to this discrete mouthpart type, however, appeared later. Metcalf et al. (1962: 141) made reference to a "chewing type: brushing, spatulate, or scraping subtype," which may not be relevant for aquatic forms, but since the authors applied the phrase to terrestrial coleopterans, it probably is transferrable to wood-boring forms and possibly leaf-miners within the mouthpart type discussed herein. James and Harwood (1969: 33) mentioned the larval "mosquito and blackfly feeding apparatus," which is largely synonymous with the "Mouthbrush Class" used in this study (Table 6). Chaudonneret (1983) used the designation, "*pièces buccales broyeuses et filtrantes*" to refer to a filter-feeding modification of the generalized mandibulate *thème* found in many aquatic dipteran larvae. A shift to a more functionally-oriented designation is found in Ross et al. (1982) with their "filtering type" and Smith (1985) who described these mouthparts as "filter-feeding" (Table 6).

I have decided to use the term "mouthbrush" as a morphological term for characterizing the mouthparts discussed herein. The term was first used in unhyphenated and unjoined form as a collective descriptor of many brushlike mouthpart structures in culicine mosquitoes by Nuttall and Shipey (1901) and Salem (1931). Salem apparently used "mouth brush" synonymously with "feeding-brush" in his 1931 article. The more mouthpart-specific term "brush," also is traceable to Nuttall and Shipley (1901) and was incorporated by Imms (1907), Shalaby (1956, 1957a, 1957b), Snodgrass (1959) and others in important descriptions of culicid mouthparts. During this time and soon thereafter the term "brush" became adjectively qualified to refer to specific mouthpart structures, including labral brushes (Shalaby 1957b, Manning 1978), mandibular or prosthecal brushes (Pao and Knight 1970, Knight 1971, Craig 1977, Harbach 1977) and palatal brushes (Craig 1974a, Davis 1974, Borkent and Wood 1986), among others. Because of its general reference to a type of mouthpart structure ubiquitously found in most major mouthpart elements of larval nematocerans and because of its early usage in culicid mouthpart studies, I am designating the term **mouthbrush** for this mouthpart grouping.

Review of Literature. A substantial literature exists for description of micro- and macrostructure, functional morphology and feeding habits of the Mouthbrush Class. Much of this literature is relatively recent, dating from the 1950's to the present, and is centered on culicids and to a lesser degree on chironomids and simuliids. Much of the classic descriptive literature has been replaced by recent research documenting SEM ultrastructure of cephalic fans and fan meshwork, executing cinematographic studies of particle flow and particle capture and describing mouthpart mechanisms of particle capture and engulfment.

Literature sources describing head and mouthpart morphology of additional species of the Mouthbrush Class include Peterson's (1951) general account of head and mouthpart structure for all families in the class, Snodgrass' (1959) discussion of the head and mouthpart structure and feeding types of several culicine genera and Pucat's (1965) documentation of several representative culicid and chaoborid species and their feeding mechanisms. Smith (1985) has provided a succinct functional morphological account of filtering mechanisms.

Studies focusing on particular mouthpart elements include Barraud and Covell's (1928) review of buccal cavity structure in several culicid species, Knight's (1971) and Harbach's (1977) comparisons of mandibulate dentition and brush development among representative culicid, chaoborid and dixid genera, and Harbach's (1978) comparative study of labiohypopharynges. Besides Wirth and Stone's (1956) account, recent family-based accounts can be found in Alexander and Byers (1981) and Byers (1984) for Tipulidae, Wood (1981b) for Pachyneuridae, Hardy (1981) for Bibionidae, Steffan (1981) for Sciaridae, Alexander (1981b) for Bibionidae, Steffan (1981) for Sciaridae, Alexander (1981b) for Trichoceridae, Alexander (1981c) for Ptychopteridae, Peters (1981) for Dixidae, Cook (1981) for Chaoboridae, Stone (1981) and Newson (1984) for Culicidae, Stone and Peterson (1981) for Thaumaleidae, Oliver (1981) and Coffman and Ferrington (1981) for Chironomidae and Peterson (1981b, 1984) for Simuliidae.

Documentation of mouthpart and head structure and feeding habits of larval culicids is extensive, principally because of the role adult mosquitoes play as vectors of various pathogens affecting humans in the tropics and subtropics. These include malaria, transmited by *Anopheles*, and yellow fever, dengue, encephalitis and filariosis, transmitted by *Aedes* and *Culex* (see Gillott 1980: 664). Studies describing *Aedes* mouthpart and head morphology include Shalaby (1957a) for *A. aegypti*

(Linneaus), Gardner, Nielsen and Knight (1973) for *A. communis* (DeGeer), and Pao and Knight (1970) for *A. vexans* (Meigen). For *Anopheles*, similar studies are Schremmer (1950a) for *A. maculipennis* Meigen, and Farnsworth (1947), Shalaby (1956) and Menees (1958) for *A. quadrimaculata* (Say). Mouthpart and head structures of *Culex* have been described by Chaudonneret (1962, 1965) for *C. pipiens* (Linneaus) and Shalaby (1957b) for *C. quinquefasciatus* (Say). Sources discussing particular culicid mouthpart elements are Gardner and Nielsen (1973) for mouthpart dentition and setation of *Aedes*, Manning (1978) for SEM's of mouthpart and filter-fan ultrastructure, and Merritt and Craig (1987) for elucidating mucous production in fine particle capture. Cook (1944b) has presented a general survey of the mouthparts and head structures of four representative culicid genera.

Adult simuliids, or black flies, are serious sanguinivorous pests of humans and domestic animals, and transmit several major diseases. Thus their study has been a concern of many economic entomologists. Discussions of mouthpart and head structures are provided by Davies (1974) for *Crozetia crozetensis* (Womersley), Borkent and Wood (1986) for *Parasimulium stonei* Peterson, Craig (1977) for *Simulium tahitiense* Edwards, and Craig (1974, 1977) and Craig and Chance (1982) for *Simulium vittatum* Zetterstedt. Additional documentation can be found in Fortner (1937) for mouthpart structure in *Simulium* sp., Chance (1970) for particle size partitioning in four species of simuliids, and Ross and Craig (1980) for use of mucous in particle capture. Craig (1974) and Borkent and Wood (1986) compare the cephalic fan structure of several simuliid genera. The biomechanics of particle capture under specified flow regimes have been demonstrated by Ross and Craig (1980), Chance and Craig (1986) and Braimah (1987a, 1987b).

Chironomid larval mouthparts have been extensively studied because of their major role as filter-feeders in freshwater ecosystems. Descriptions of the heads and mouthparts of particular species can be found in Leathers (1922) for *Chironomus braseniae* Leathers, in Gouin (1957) for *Chironomus plumosus* Linneaus, by Cook 1944c) for an unidentified species of *Chironomus*, by Burtt (1940) for *Glyptotendipes glaucus* (Meigen), and by Müh (1985) for *Macropelopia nebulosa* (Meigen). Additional mouthpart references on *Chironomus* Miall and Hammond (1892), Walshe (1947) and Gouin (1959). Gouin (1959) and Oliver (1981) provide general reviews of chironomid mouthparts and feeding habits.

Discussions of mouthpart and head structure for dixids occur in Smith (1928), Schremmer (1950b) and Felix (1962). Among chaoborids, Colless (1977) has described a unique filtering mechanism in *Australomochlonyx nitidus* Freeman, and Giguère and Dill (1983) have documented the feeding cycle of *Chaoborus trivittatus* Loew by cinematography. For tipulids, Cook (1949) and Snodgrass have described the head and mouthparts of species of *Tipula*, and Chiswell (1955) has done likewise for *Tipula livida* Van der Wulp. Ptychopterid mouthpart and head structures are documented by Kramer (1954) for *Bittacomorpha* sp. and Hodkinson (1973) for *Ptychoptera lenis* Osten Sachen. Keilen (1940) has described similar structures for the trichocerid, *Trichocera hiemalis* (DeGeer).

Descriptions of buprestid larval head and mouthpart structures include Böving and Craighead (1931) and Peterson (1951) for *Chrysobothris femorata* Oliver and *Chalcophora virginiensis* Drury. For the leaf-miner *Gracillaria stigmatella* Fabricius, useful descriptions were provided by Tragardh (1913), DeGryse (1915) and MacKay (1972). The leaf-miner *Phyllocnistis suffusella* Zeller was described by Tragardh (1913), Jayewickreme (1940) and Grandi (1959).

This literature review covers only a minor portion of the numerous studies investigating mouthpart and head structure of the Mouthbrush Class. Because of a recent upsurge of research in this mouthpart class, structural descriptions and functional-morphological documentation probably will increase disproportionately, when compared to other mouthpart classes.

8.3.13. Mandibulobrustiate Class
(Class 12)

Description. Head nonproboscate, spheroidal to anteriorly prolonged. Genae dorsally and ventrally expanded, comprising most of cranium; gular region prominent to moderately developed. Frontoclypeus wide and triangular, demarcated by an inverted Y-shaped epistomal suture. Antennae short and stubby, or absent; lateral ocelli present (often grouped as stemmata); compound eyes absent. Mouthparts mandibulate, prognathous or hypognathous, symmetrical, non retractile. Food pump evidently pharyngeal.

Clypeus quadrate to vertically elongate; fused to frons. Labrum vertically elongate, rarely quadrate or transversely elongate; undivided; margin pectinate or infrequently straight to curvilinear or penicillate. Hypopharynx bilobed, with lateral brushes associated with labiomaxillary spinneret; epipharynx membranous. Mandibles dicondylic;

pyramidal to rarely falcate; acuminately incisiform, often with brush or setal tuft in molar region; musculation typical of adduction/abduction. Maxilla with main-body divided into 3 sclerites; stipes elongate; bearing a lacinia and palpus. Maxillary palpi mucronate; 4-segmented; short to intermediate in length. Lacinia a falcate pectinate comb with mesially directed setae or spines, or fimbriate; galea absent. Labium main-body equant to elongate, subdivided into two sclerites; bearing glossae and palpi. Labial palps papillate/stubby or mucronate; 1- to 3-segmented; short in length. Glossae a hypopharynx-associated spinneret fused with maxillae to form a labiomaxillary complex; paraglossae absent. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. The major diagnostic character of the Mandibulobrustiate Class is a distinctive pyramidal mandible with an incisiform distal region and a variously developed brush or brushlike structure occurring mesially in the molar region. Second, a labiomaxillary complex housing a spinneret is present, although this feature is also present in the Sericterate Class (Section 8.3.14). Galeae are absent and most head appendages are either extremely reduced or dimunitive and stubby in form.

Although this mouthpart class is moderately stereotyped, it exhibits some common features with other mouthpart classes characterized by a derived, holometabolous larval facies. The Mandibulobrustiate Class is most similar to the terrestrial Sericterate Class but can be differentiated from it by mouthpart structures, especially brushes, related to feeding in the aquatic realm. It can be differentiated from the Pectinate Class (Section 8.3.11) by its holometabolous larval facies, differences in head shape and mouthpart vestiture that is beset with brushlike rather than pectinate or spinose processes. Mandibular brushes, often in the form of prosthecae, are found in adult floricolous beetles (Bertin 1923, Blackwelder 1934, Barth 1985; see Section 6.9.3) but their adult head structure nevertheleess departs significantly from the holometabolous larval facies of the Mandibulobrustiate Class.

Diversity and Natural History. The Mandibulobrustiate Class consists of all larval stages of trichopterans, a group of holometabolous insects that are almost exclusively aquatic (only a few terrestrial forms are known) and are a major ensemble of primary consumers in freshwater ecosystems (Wallace and Merritt 1980, Anderson and Cargill 1987). Mandibulobrustiates occur in lotic and lentic habitats and on various substrates, particularly mud, sand, rocky bottoms, submerged vascular hydrophytes, moss, filamentous algae and even sponges (Wiggins 1984). Members of this mouthpart class are either climbers, sprawlers or clingers (Cummins and Merritt 1984) and construct either (i) fixed burrows with silken tube retreats, (ii) portable, silk-wolven larval cases of various mineralic and plant substrates and geometric designs, or (iii) silk nets of various shapes and meshes in fixed retreats (Sattler, 1958, Wallace and Malas 1976, Merritt and Wallace 1981, Wiggins 1984). Some forms are free-living and lack larval retreats or larval cases (Wiggins 1984).

Mandibulobrustiates consist of 0.74% of all insects and are a moderately diverse group taxonomically, comprising 39 families, about

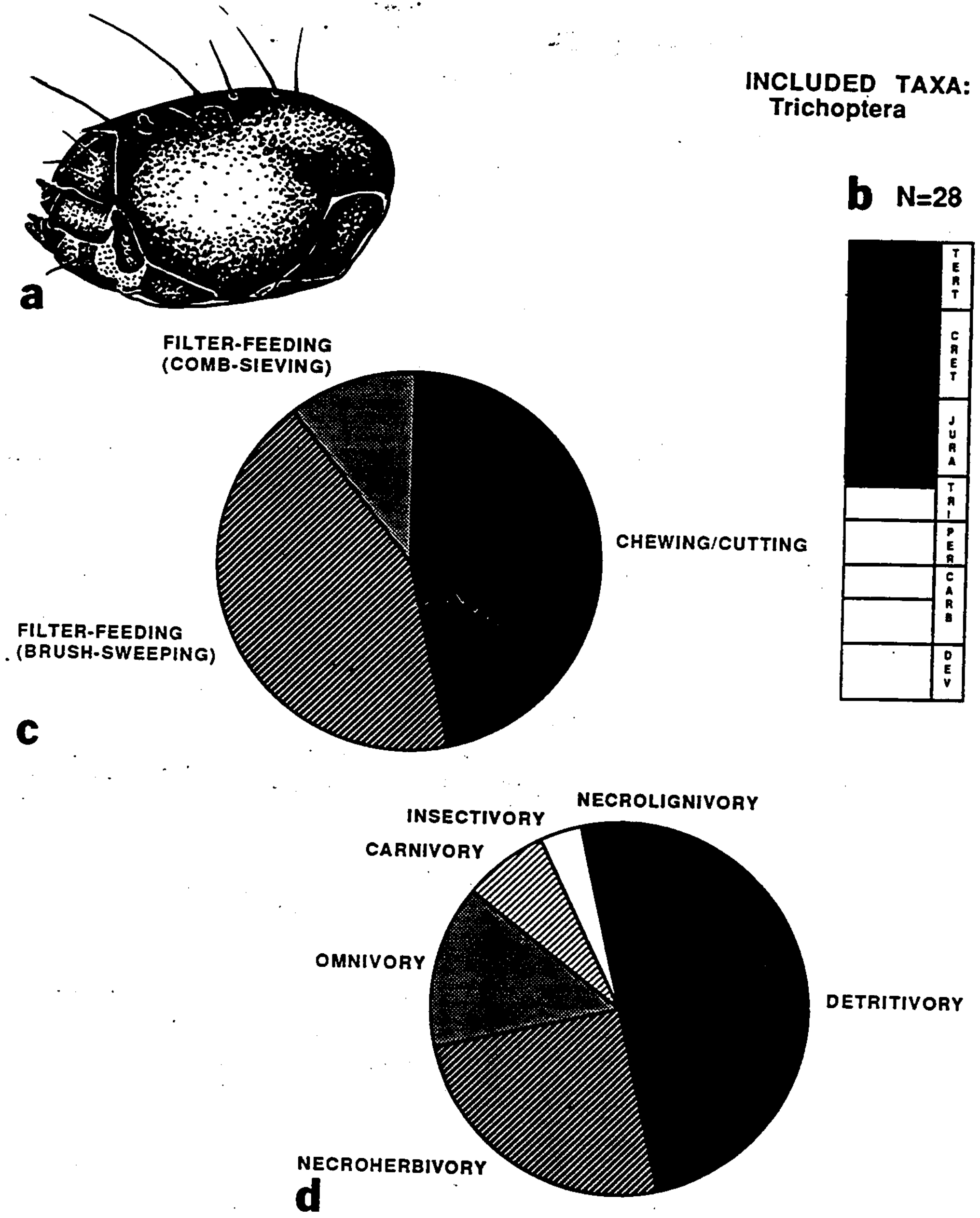


FIGURE 62. Overview of the Mandibulobrustiate Mouthpart Class. a, *Limnephilus flavicornis* Fabricius (Trichoptera: Limnephilidae, dataset no. 1059), after Winkler (1959); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

630 genera and about 6600 species (Appendix D). This diversity translates to a rank-order of 17 among 34 mouthpart classes (Table 5, Fig. 131). Most members are herbivores of one type or another (Fig. 62) and exhibit minimal food selectivity (Slack 1936, Hickin 1967, Wallace and Merritt 1980). In terms of functional-feeding-groups, they are characterized by the following five categories: collector-filterers, collector-gatherers, scrapers, shredders (both herbivorous and detritivorous versions) and predator-engulfers (Cummins 1973, Cummins and Klug 1979, Wiggins 1984). A few are "piercers" (Wiggins 1984) that lack stylate mouthparts and, because of their very small size, are able to puncture individual algal cells using nominal mandibulate mouthparts. A common theme of this group is the use of mouthpart-spun silk for net construction or as a building material for burrow lining or larval cases (Wallace and Merritt 1980).

Structural Themes. Mandibulobrustiates are characterized by six major subclusters (Fig. 63). The phenetic pattern of mandibulobrustiate mouthparts is a large central subcluster encompassing almost all trichopteran families (bracketed by data-set nos. 1033 to 1076 in Fig. 63) and five structurally divergent families occurring as segregates outside this central subcluster. The dominance of this central subcluster is reflected in the character-state distributions of relevant characters: for each character one or rarely a few character-states supports the central subcluster and invariably another character-state of the same character supports one of the segregate subclusters. Although 16 characters provide most of the structure to the subclustering

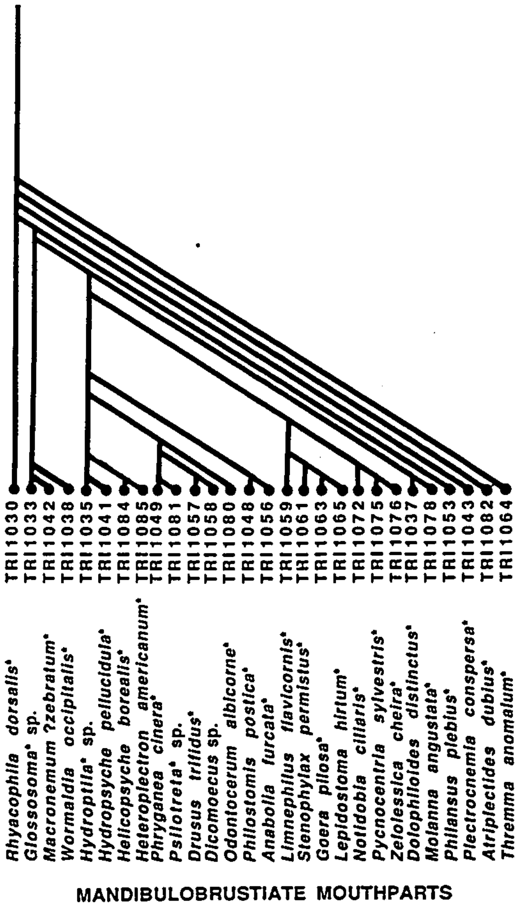

Rhyacophila dorsalis* TRI1030
Glossosoma* sp. TRI1033
Macronemum ?zebratum* TRI1042
Wormaldia occipitalis* TRI1038
Hydroptila* sp. TRI1035
Hydropsyche pellucidula* TRI1041
Helicopsyche borealis* TRI1084
Heteroplectron americanum* TRI1085
Phryganea cinera* TRI1049
Psilotreta* sp. TRI1081
Drusus trifidus* TRI1057
Dicomoecus sp. TRI1058
Odontocerum albicorne* TRI1080
Philostomis postica* TRI1048
Anabolia furcata* TRI1056
Limnephilus flavicornis* TRI1059
Stenophylax permistus* TRI1061
Goera pilosa* TRI1063
Lepidostoma hirtum* TRI1065
Notidobia ciliaris* TRI1072
Pycnocentria sylvestris* TRI1075
Zelolessica cheira* TRI1076
Dolophilodes distinctus* TRI1037
Molanna angustata* TRI1078
Philansus plebius* TRI1053
Plectrocnemia conspersa* TRI1043
Atriplectides dubius* TRI1082
Thremma anomalum* TRI1064
MANDIBULOBRUSTIATE MOUTHPARTS

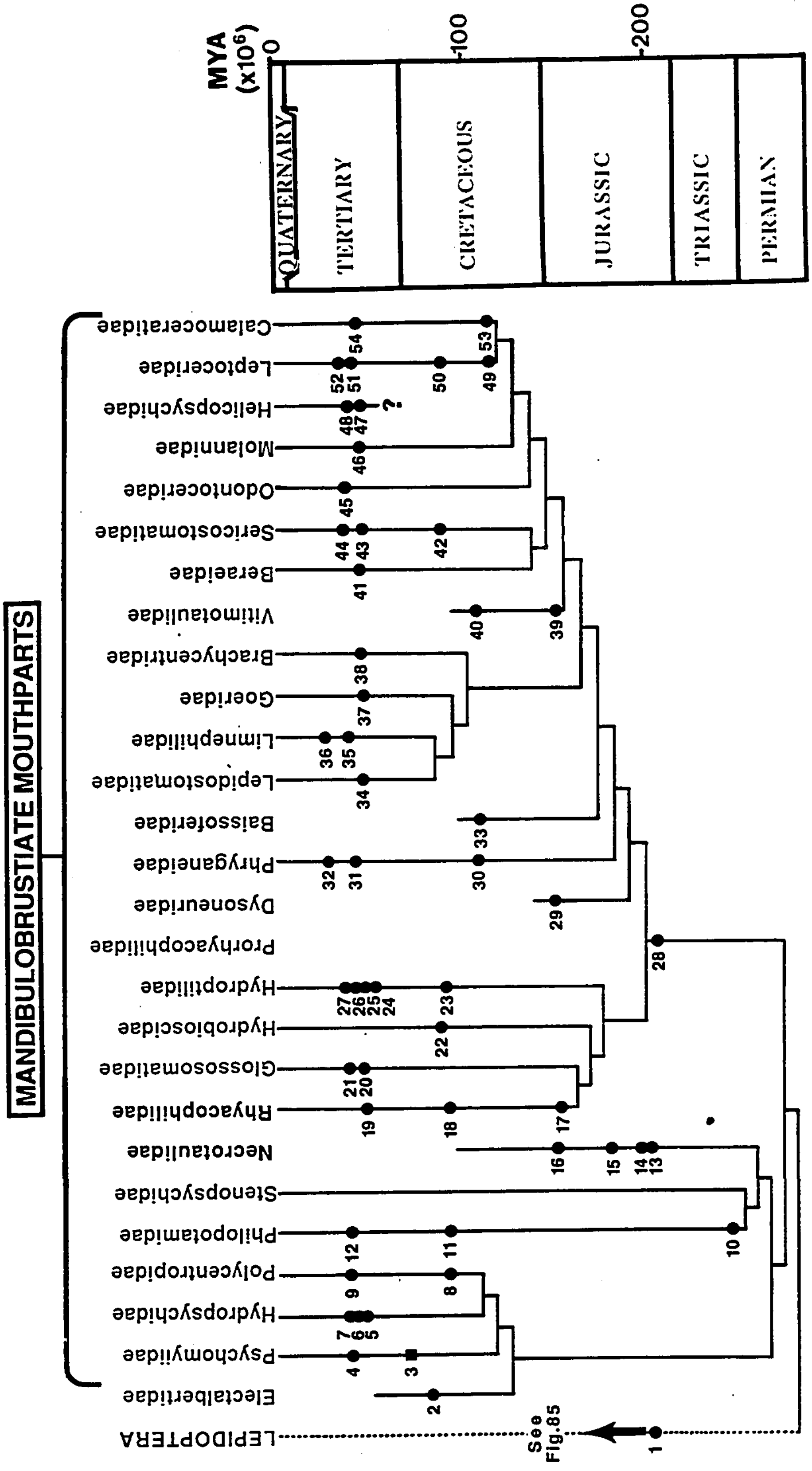
FIGURE 63. Cluster analysis dendrogram of taxa comprising the Mandibulobrustiate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

pattern, several of these are uniform throughout five of the six subclusters, and they only provide resolution for one of the five monotaxic subclusters (*vide infra*). The important characters are genal region/malar space development, antennal type, ocelli or stemmata number, compound eye presence, mouthpart placement, mouthpart symmetry, clypeal shape and segmentation, labral margin modification, epipharynx type, mandible type, mandibular dentition, maxillary palpus segmentation and aspect ratio, paraglossal modifications and labial participation in a multielement mouthpart structure.

Subcluster 1 consists of the free-living, predatory rhyacophilid *Rhyacophila dorsalis* (data-set no. 1030). Subcluster 2 is the taxonomically diverse suite of 24 taxa from all superfamilies and most families of trichopterans; this subcluster exhibits three major subgroupings. Members of this subcluster construct larval cases, occasionally are net-spinners and are dominately herbivorous or detritivorous in feeding habits. Distantly associated subclusters include the unique, semiparasitic, marine form *Philansus plebius*, a chathamiid (Subcluster 3, 1053), the polycentropid *Plectrocnemia conspersa* (Subcluster 4, 1043), the atriplectrid *Atriplectides dubius* (Subcluster 5, 1082) and the thremmatid *Thremma anomalum* (Subcluster 6, 1064). These monotaxic subclusters are generally poorly known and have been documented relatively recently.

Geochronologic History. The time of origin of trichopterans, and hence mandibulobrustriates, is difficult to assess. Depending on the author, the earliest identifiable trichopteran fossils range from the

FIGURE 64. Geochronologic history of the Mandibulobrustiate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Ross (1967), Sukacheva (1982) and Botosaneanu and Wichard (1983). The taxonomic level of analysis is the family; without fossil representatives are omitted. The outgroup is Lepidoptera. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.


MYA (x10⁶)
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
MANDIBULOBRUSTIATE MOUTHPARTS
Calamoceratidae
Leptoceridae
Helicopsychidae
Molannidae
Odontoceridae
Sericostomatidae
Beraeidae
Vitimotaulidae
Brachycentridae
Goeridae
Limnephilidae
Lepidostomatidae
Baissoferidae
Phryganeidae
Dysoneuridae
Prorhyacophilidae
Hydroptilidae
Hydrobiosidae
Glossosomatidae
Rhyacophilidae
Necrotaulidae
Stenopsychidae
Philopotamidae
Polycentropidae
Hydropsychidae
Psychomyiidae
Electalbertidae
LEPIDOPTERA
See Fig.85
?

Lower Permian (Sukacheva 1976, 1982) to Lower Cretaceous (Hennig 1981). Several reasons exist for this uncertainity, foremost of which is the insensible gradations of wing venation among the following members of the panorpoid complex (Table 1): relatively derived Permian mecopterans, several enigmatic panorpoid fossils of the Permian and Triassic (e.g. *Belmontia*, *Eoses*), Recent rhyacophilid trichopterans and Recent micropterygid lepidopterans (Shields 1988). A second reason is the absence of trichopterous larvae in Paleozoic or Early Mesozoic strata. this absence is noteworthy since all of the "constitutive characters" (Hennig 1981) occur on larvae rather than adults (Ross 1967, Hennig 1981). For example, there are considerably more differences between trichopteran and lepidopteran larvae than between adults of the same groups (Shields 1976, Whalley 1978, Boudreaux 1987). The earliest known larval fossil is a case from the Upper Jurassic, although larval cases do not enter the fossil record with abundance until the Lower Cretaeous [53,52] (Sukacheva 1968, 1982; Jell and Duncan 1986).

During the Early Permian there occurred three families of seemingly derived mecopterans that have been reassigned to the suborder Permotrichoptera of the Trichoptera (Riek 1953, Sukacheva 1976). If this assignment is valid, then the earliest documented trichopterans are Lower Permian (Fig. 64) and include *Platychorista venosa* Tillyard 1926 of the Protomeropeidae (=Platychoristidae) from Kansas [90] and *Kamopanorpa pallida* Sukacheva 1976 of the Microptysmatidae from the USSR [89] (Sukacheva, in Rohdendorf and Rasnitsyn 1980). Whereas some authors accept referral of at least some of these and other fossils to the Trichoptera (Riek 1970, Whalley 1978, Wootton 1981, Carpenter and Burnham 1985), others are sceptical, maintaining that they are members of the stem-group Amphiesmenoptera (=Trichptera + Lepidoptera) (Hennig 1981, Wootton 1988, Williams 1988).

Presumed trichopterous fossils from the Triassic are more differentiated, albeit venational details can be interpreted as indicating mecopteran, trichopteran or lepidoptean affinities. Examples include *Eoses triassica* Tindale 1945 and *Eocorona iani* Tindale 1980 from the Middle Triassic of Queensland, Australia [79]. These species are claimed by Tindale (1945, 1980) as true lepidopterans and by Riek (1955), Hennig (1981), Skalski (1984) and Shields (1988) variously as mecopterans, amphiesmenopterans, or as trichopterans (see Razowski 1974). In the same deposit occurs *Prorhyacophila colliveri* Riek 1970, which according to Shields (1988), probably represents the earliest trichopteran. This form resembles the Rhyacophilidae (Sukacheva 1973), the most primitive extant trichopteran group, and is characterized by a free-living larva and a venation similar to micropterygid lepidopterans and *Eoses* (Ross 1967, Whalley 1978, Common 1975, Shields 1988). However this fossil post dates a fossil member of the extant family Philopotamidae (*Prephilopotamus asiaticus* Sukacheva 1973) found in the Upper Madygan Suite of Early Triassic age [82] of the USSR (Sukacheva 1973). This exceptional find not only places the earliest identifiable trichopteran and mandibulobrustiate as Early Triassic, but it deflects the problems of establishing the presence of Early Mesozoic trichopterans based on vague venational characters borne by members of several orders within the panorpoid facies.

Jurassic insects referred to the Trichoptera are mostly members of the extinct annulipalpian family, Necrotaulidae, and occur from the Late Triassic to Late Jurassic of Europe and South America (Tillyard 1933, Riek 1970, Shields 1988). Ross (1967) and Hennig (1981) doubted whether necrotaulids were trichopterous, preferring to assign the family to the Amphiesmenoptera. With the exception of the Early Triassic philopotamid described above, it is not until the Early Cretaceous that trichopteran fossils can be identified as modern families.

From Lower Cretaceous strata from Transbailkalia of the USSR [52] Sukacheva (1968, 1982) has documented wings and larval cases allied to the Recent annulipalpan Polycentropidae and Rhyacophilidae and the Recent integripalpan Brachycentridae and Lepidosomatidae. Jell and Duncan (1986) have identified a calamoceratid pupa and a leptocerid larval case from the Lower Cretaceous of southern Australia [53]. Additionally Lewis (1971) has described a probable limnephilid larval case from the Upper Cenomanian/Turonian stage from the Windrow Formation of Minnesota. Upper Cretaceous trichopteran fossils are found principally in ambers of Cedar Lake, Canada [35] and northern Siberia [37]. Some described species from these two deposits belong to extant genera of the Rhyacophilidae, Polycentropidae, Hydrobiosidae, Leptoceridae and Calamoceratidae or Odontoceridae (Botosaneanu and Wichard 1983, 1984). Ross (1958) has documented a Cretaceous (stage unspecified) philopotamid from Tennessee amber [25] that is related to modern cool-adapted forms.

The major source of Cenozoic trichopterans is Baltic amber [19], from which Ulmer (1912) has described over 56 genera and 152 species (Larsson 1978).

Previous Designations. I am using the new designation, **mandibulobrustiate** to refer to the pervasive presence of a brush (Latin: *brustium*) on the mesial aspect of the mandibles and thus as a name for the mouthbrush discussed herein. This feature that characterizes virtually all members of the mouthpart class. (A few predatory forms, however, lack mandibular brushes.) Additionally, rows of tufts of setae, brushes, or two long setae may occur along the curved, lateral margin of each mandible. These features are the single most diagnostic feature of the mandibulobrustiate mouthpart class and distinguish it from the coarsely setate mouthpart vestiture found in the pectinate and mouthbrush mouthpart classes (Sections 8.3.11 and 8.3.12). Although the term "mandibulobrustiate" has no prior history of usage, Metcalf et al. (1962: 141) defined one mandibulate mouthpart group as the "chewing type: brushing, spatulate or scraping subtype" which may have included members of this mouthpart class (Table 6).

Review of Literature. General summaries of head and mouthpart structure of members belonging to the mandibulobrustiate class include, for North America, Lloyd and Lloyd (1921), Krafka (1923), Wiggins (1977, 1984), and Morse and Holzenthal (1984). Hickin (1967) has provided a summary of British caddisfly larvae.

Monographic accounts of the head and mouthpart morphology of particular species are provided for most major groups and are generally copious for limnephilids. Documentation for most or all features of the head and mouthparts include Sattler (1959) for the hydropsychid *Hydropsyche* sp., Botosaneanu (1956) for several species, namely the rhyacophilid *Rhyacophila laevis* Pictet, the limnephilid *Drusus romanicus* Murgoci, the goerid *Silo varipilosa* Botosaneanu and the philopotamid *Wormaldia occipitalis* Pictet, Fotius-Jaboulet (1961) for the limnephilid *D. trifidus* MacLachlan, Winkler (1959) for the limnephilid *Limnephilus* sp., Wiggins (1959) for the phryganopsychid *Phryganopsyche latipennis* (Banks), Frochot (1962) for the limnephilid *Stenophylax permistus* MacLachlan and Satija and Satija (1959) for the philopotamid *Wormaldia occipitalis* Pictet. Relatively recent contributions include Wiggins (1977, 1984) for the glossosomatid *Glossosoma*, Wiggins (1977) and Morse and Holzenthal (1984) for the hydroptilid *Hydroptila* sp., Hickin (1968) and Cowley (1978) for the polycentropid *Plectrocnemia* sp. and Cowley (1978) for the coeoesucid *Pycnocentria sylvestris* McFarlane and the helicophid *Zelolessica cheira* McFarlane. The unique marine chathamiid, *Philanisus plebius* (Walker), has been briefly described by Leader (1976) and Lawson-Kerr (1977) and Cowley (1978). More specialized accounts have been provided by Slack (1936) for mandibles, Wiggins (1960) for pupal mandibles and Badcock (1961) for the labiomaxillary apparatus of hydropsychids.

8.3.14. Sericterate Class
(Class 13)

Description. Head spheroidal, less commonly marginally projecting; nonproboscate; generally protractile. Genae expanded dorsoventrally, comprising most of the cranium; gula prominent to minimally developed. Frontal and vertical region wide and triangular, with an inverted Y-shaped epistomal suture, less commonly unexpanded. Antennae papillate, setigerous or stylate; ocelli 2, and many lateral stemmata often present; compound eyes absent. Mouthparts mandibulate, prognathous or hypognathous, symmetrical, nonretractile. Food pump generally clypeal and pharyngeal.

Clypeus quadrate to transversely elongate; undivided or fused to frons; rarely absent. Labrum vertically elongate, less commonly quadrate; undivided; margin pectinate, notched or straight to shallowly curvilinear. Pharyngeal cavity large; hypopharynx bilobed, associated with a labial spinneret; epipharynx membranous or lingulate, rarely denticulate or spinose. Mandibles dicondylic; palmate to rarely falcate or triangular; incisiform, uncommonly edentate or with a prominent mesial brush; musculation of adduction/abduction mode. Maxillary main-body of 1 to 3 sclerites; stipes equant, less commonly elongated; bearing a galea and palpus only, or less commonly a galea, lacinia and palpus, or rarely a palpus only. Maxillary palps stubby or papillate, uncommonly linear-tapering; 2- or 3-segmented, rarely 4-segmented or unsegmented; length short to commonly intermediate. Galea lobate, sensillate and setate, less commonly generalized or palpiform; lacinia mostly absent, rarely generalized or pectinate. Labium main-body equant or considerably elongated, of 2 or 3 sclerites; bearing a spinneret associated glossa and labial palps. Labial palps papillate-stubby or aciculate to setate, rarely mucronate; generally unsegmented or

2-segmented, rarely 3-segmented; generally short. Glossae or ligulate projection bearing a terminal spinneret (silk press); paraglossae absent or indistinguishably fused to glossae. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. A diagnostic feature of sericterates is a moderately-sized to large head with pronounced genae forming most of the head capsule. The head capsule is also characterized by a prominent, Y-shaped epistomal suture. Additionally, a characteristic labiohypopharyngeal complex bears a stubby ligula containing the spinneret and two papillate or aciculate labial palpi. In the majority of members which are herbivorous, the mandibles are palmate, with several incisors and a poorly-developed or absent molar region; mandibles of nonherbivorous species are falcate or more typically tetrahedral in shape.

This suite of characters uniquely define the sericterate mouthpart class and could only be confused with larval ectognathates (Section 8.3.5) and mandibulobrustiates (Section 8.3.13). Larval-ectognathates lack the labiohypopharyngeal apparatus of the spinneret. Mandibulobrustiates differ from sericterates by the presence of conspicuous brustia and setae on the mouthparts and the absence of stereotyped palmate or falcate mandibles.

Diversity and Natural History. Sericterates consist of the eruciform larvae of lepidopterans and symphytan hymenopterans (commonly known as caterpillars), as well as the apodous larvae of apocritan hymenopterans (often referred to as grubs). Sericterates are chiefly herbivores, consuming every major type of plant tissue, including roots, stems, leaves, flowers, seeds and fruits (Fig. 65). A few, less diverse sericterate groups are endoparasitic, mostly on other insects (Malyshev 1968, Telenga 1969) or are provisioned and cared for by conspecific adults in social and subsocial groups (Wilson 1975). Nevertheless about 70% of this mouthpart class comprises the dominant assemblage of herbivores on virtually all land plants, particularly angiosperms. Sericterates comprise the following functional feeding groups: external foliage chewers (including leaf skeletonizers), leaf-miners (but also see Section 8.3.12), leaf-gallers, stem- and root-borers, ectoparasitoids, endoparasitoids and free-feeding necrovores with food provisioned by conspecific adults. Many sericterates are agricultural and stored-product pests.

Of the major taxonomic orders of insects that consume plants, three are noteworthy in abundance and diversity. These are lepidopterans (99% herbivorous, about 136,000 species), coleopterans (34.5% herbivorous, about 118,000 species) and orthopterans (99% herbivorous, about 18,000 species) (Brues 1920, Strong et al. 1984; Appendix D). Of these three groups, larval lepidopterans and the morphologically similar larval symphytan hymenopterans, are probably the most important single, identifiable insect group consuming angiosperms (Edwards and Wratten 1980, Strong et al. 1984, Tabashnik and Slansky 1987). The sericterate mouthpart class is very diverse, corresponding to approximately 170 families, 20,000 genera and 259,300 species (Appendix D), which translates to a rank-order of 3 out of 34 mouthpart classes (Table 5, Fig. 131). Thus, sericterates rival but are subdominant to adult-ectognathates (Section 8.3.4) and larval-ectognathaes (Section 8.3.5) in

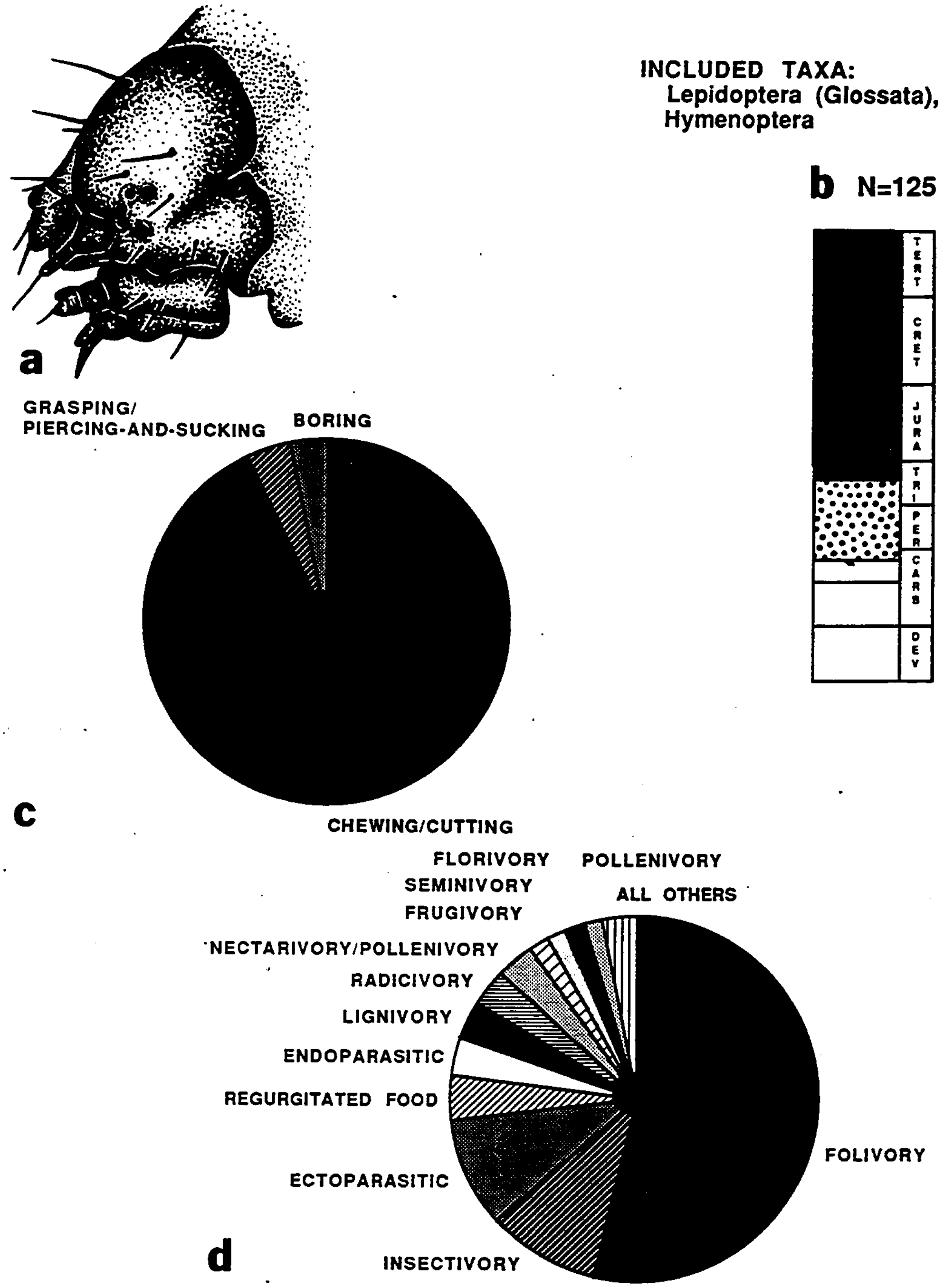


FIGURE 65. Overview of the Sericterate Mouthpart Class. a: *Gnorimoschema* sp. (Lepidoptera: Gelechiidae, data-set no. 1137), after Peterson (1948); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

terms of total diversity and is probably the second most important class overall on terrestrial vegetation.

Significantly, many studies indicate that sericterates are the dominant of subdominant group consuming herbaceous, shrubby or arboreal vegetation. On *Baccharis* (Asteraceae), Palmer (1987) documented stem-borers, root-feeders, stem-gallers, leaf-mines, foliage-feeders and flower-feeders as part of the lepidopteran fauna. Ashbourne and Putnam (1987) have categorized sericterate-dominated herbivory, distinguishing discrete subcategories of leaf-mining, leaf-galling and vein-chewing as feeding strategies of the sericterate dominated fauna. Goeden and Ricker (1987a,b) established that lepidopterans are the second most abundant consumer of American *Cirsium* thistles (Asteraceae). Hijii (1983, 1984, 1986) measured lepidopteran biomass in arboreal arthropod communities in *Cdhamaecyparis* (Cupressaceae) plantations in Japan and found that lepidopteran larval biomass ranged from 20 to 63% of total arthropod biomass. He also found that in *Cryptomeria* (Taxodiaceae) plantations the numerical abundance and biomass of lepidopteran and hymenopteran caterpillars were approximately proportional to tree size.

Much of this dominance involves the sequestering of host plants in a highly coevolved relationship between a larval consumer and its host (Southwood 1973, 1978; Jolivet 1986). Most sericterates have narrow host plant specificities, with particular species feeding on a single species, genus, or group of confamilial genera (Futuyma and Gould 1979). Of all phytophagous insects, fewer than 10% are generalists that consume plant genera from more than three families (Bernays and Graham 1988). However, this genralization often proves to be more complex upon closer examination: although many folivores are locally monophagous, they are frequently regionally polyphagous (Strong et al. 1984), and chemically well-defended plants, particularly herbs, bear more monophagous species than chemically less-protected plants, mainly shrubs and trees (Tahvanainen and Niemelä 1987, cf. Boomsma 1984). These relationships are probably related to the low nutritive quality and unpredictability of leaves in time and space, resulting in high feeding rates, the tracking of host plants, and facultative rather than obligate monophagy. Also contributing to this relationship is the diverse arsenal of insect deterrence that plants possess, namely generaly physical defenses such as small cuticular spines, adhesive trichomes and hooked barbs on leaf surfaces (Levin 1973, Edwards and Wratten 1980) and the presence of numerous secondary compounds, principally alkaloids, terpenoids, phenolics and tannins (Gilbert 1971, van Embden 1973, Swain 1976, Mattson and Scriber 1987). These compounds accumulate in plant organs, especially leaves, and are often toxic to insects at higher concentrations. However, among many angiosperms, this defensive response has been co-opted by some insect groups that exhibit obligate monophagy on those plant species or they demonstrate feeding prefences possessing specific secondary compounds that are deterrents to most potentially predating insects (Ehrlich and Raven 1964, Harborne 1977).

This example of an "arms escalation" (cf. Vermeij 1987) has actually benefitted many sericterates that have evolved secondary compound detoxification mechanisms (Frankel 1959, Ehrlich and Raven 1964, Strong et al. 1984), behavioral adaptations for avoiding secondary compounds (Needham, Tothill and Frost 1935; Jolivet 1986; Doussard and

Eisner 1987; Hulley 1988), physiological and structural mechanisms for avoiding physical entrapment or spine impalement (Gilbert 1971, Rathcke and Poole 1974) and actual metabolic incorporation of toxic compounds for use as a defense (Brower 1969, Edwards and Wratten 1980). Bernays (1981) has described the attraction to high tannin levels of certain sericterate larvae, which are induced to feed in its presence. In lieu of these plant defensive mechanisms, an alternative strategy available to some plants is simply a high regrowth capacity (see Van der Meijden et al. 1988).

The diversity of functional-feeding-groups and feeding strategies of sericterates on terrestrial vascular plants is immense (Frost 1959, Jolivet 1986). Of these, two are dominant within the mouthpart class: leaf-chewing and leaf-mining (see also Section 8.3.12 for additional leaf-miners). Within each of these modes there is considerable dietary specialization based on tissue type and on architecturally related microstructure of the leaf (Needham, Tothill and Frost 1935, Hering 1951, Lawton 1982). For external leaf-chewers, some caterpillars pefer leaf-edges, others skeletonize entire leaves and avoid vascular tissue, while others specialize on vascular tissue, consuming sap by chewing on phloem or xylem strands (Hering 1951, Edwards and Wratten 1980, Ashbourne and Putman 1984). Leaf-miners similarly partition the internal leaf habitat by tissue type, and include mesophyll feeders, palisade cell feeders, cuticle feeders and vascular strand consumers (Hering 1951, Bennet 1954, Hagen and Chabot 1986, Ashbourne and Putman 1987).

Although there is considerable partitioning of the leaf externally and internally and a multitude of plant tissue and organ types, several studies indicate that interspecific competition within tissue-specific herbivores is minimal (Rathcke 1976, Strong et al. 1984, Jermy 1985). On rare occasions, during an outbreak of a (usually pestiferous) monophagous species, intraspecific competition may become intense (Jermy 1985). These patterns may indicate that extant angiosperm niches may be undersaturated with respect to their occupation by potential consumers. This is attributable either to historical factors or to the unpredictable distribution of food resources and food quality in time and space, such that host-tracking is sufficiently a gambit that saturated diversities are never achieved.

Structural Themes. Sericterate mouthpart structure is characterized by six major subclusters (Fig. 66). These subclusters, or themes, each comprise from two to 39 constituent members and three of these themes are sufficiently diverse taxonomically that they exhibit a second level of subclustering. Although these secondary subclustering patterns are probably significant in terms of mouthpart structure within each theme, they will not be considered at the level of analysis of this discussion. The six major subclusters are differentiated by approximately ten major characters, although the patterns of character state co-occurrence among these subclusters is more complex than that of other mouthpart classes. These variables are head shape; antennal type, stemmatal number; clypeal shape; mandibular type; galeal, lacinial and glossal variations; and the type, segmentation and aspect ratio of the labial palp (see Section 5.3 and Appendix A).

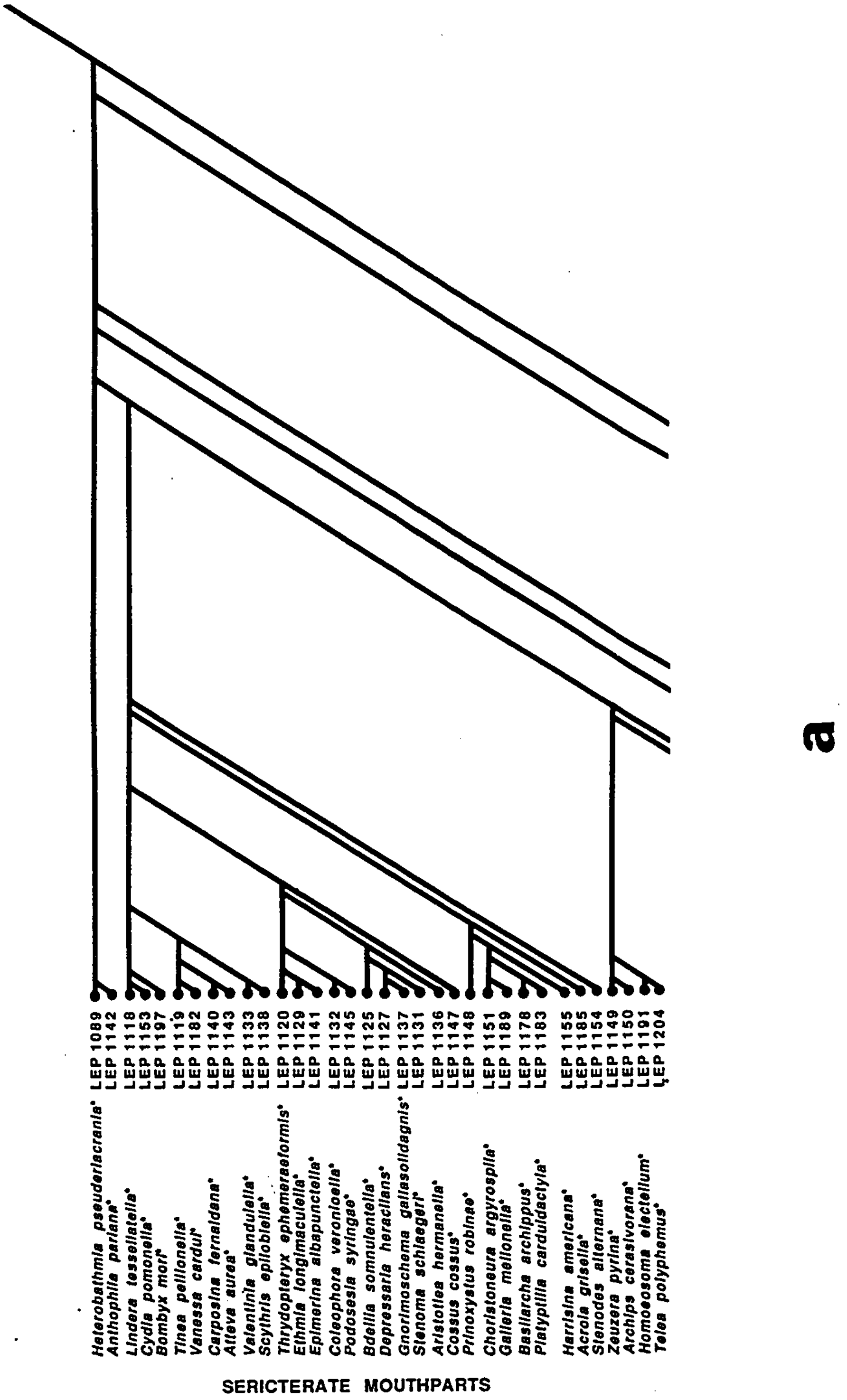
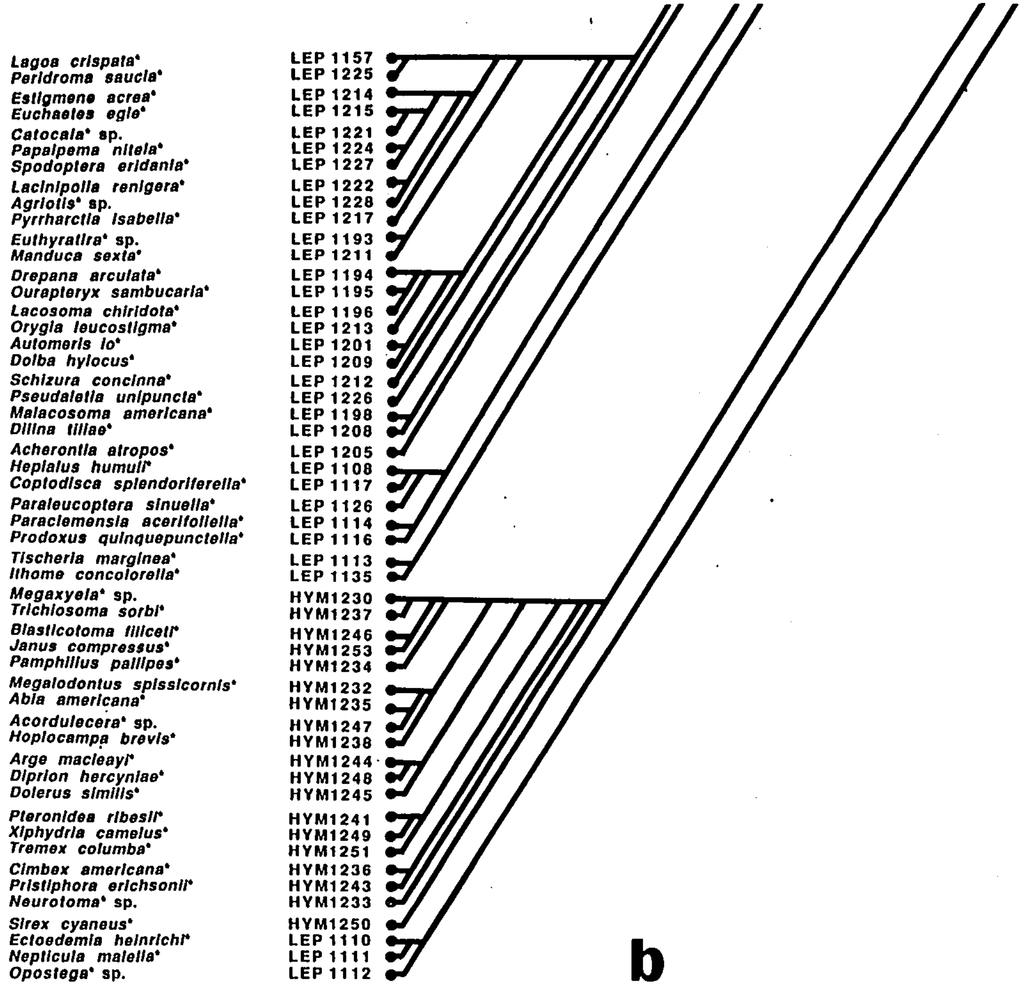
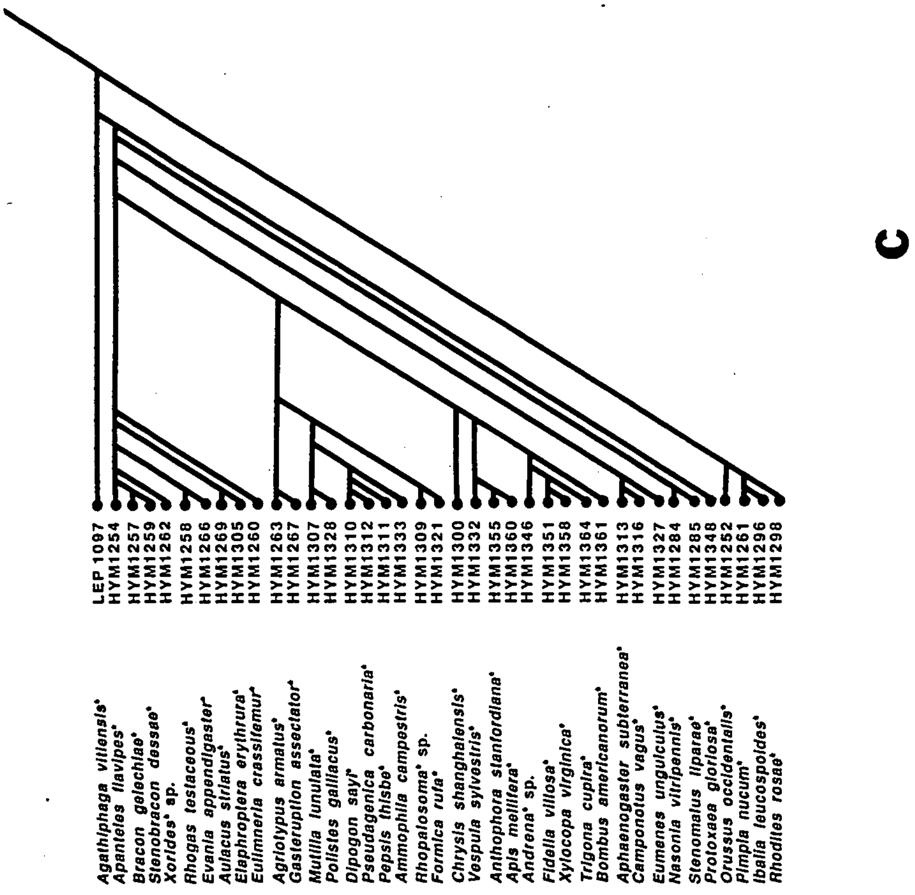

Heterobathmia pseuderiocrania* LEP 1089
Anthophila pariana* LEP 1142
Lindera tessellatella* LEP 1118
Cydia pomonella* LEP 1153
Bombyx mori* LEP 1197
Tinea pellionella* LEP 1119
Vanessa cardui* LEP 1182
Carposina fernaldana* LEP 1140
Atteva aurea* LEP 1143
Valentinia glandulella* LEP 1133
Scythris epilobiella* LEP 1138
Thrydopteryx ephemeraeformis* LEP 1120
Ethmia longimaculella* LEP 1129
Epimerina albapunctella* LEP 1141
Coleophora veronioella* LEP 1132
Podosesia syringae* LEP 1145
Bdellia somnulentella* LEP 1125
Depressaria heraclians* LEP 1127
Gnorimoschema gallasolidagnis* LEP 1137
Stenoma schlaegeri* LEP 1131
Aristotlea hermanella* LEP 1136
Cossus cossus* LEP 1147
Prinoxystus robinae* LEP 1148
Choristoneura argyrospila* LEP 1151
Galleria mellonella* LEP 1189
Basilarcha archippus* LEP 1178
Platyptilia carduidactyla* LEP 1183
Harrisina americana* LEP 1155
Acroia grisella* LEP 1185
Stenodes alternana* LEP 1154
Zeuzera pyrina* LEP 1149
Archips cerasivorana* LEP 1150
Homoeosoma electellum* LEP 1191
Telea polyphemus* LEP 1204
SERICTERATE MOUTHPARTS
a

FIGURE 66. Cluster analysis dendrogram of taxa comprising the Sericterate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

SERICTERATE MOUTHPARTS


Lagoa crispata* LEP 1157
Peridroma saucia* LEP 1225
Estigmene acrea* LEP 1214
Euchaetes egle* LEP 1215
Catocala* sp. LEP 1221
Papaipema nitela* LEP 1224
Spodoptera eridania* LEP 1227
Lacinipolia renigera* LEP 1222
Agriotis* sp. LEP 1228
Pyrrharctia isabella* LEP 1217
Euthyratira* sp. LEP 1193
Manduca sexta* LEP 1211
Drepana arculata* LEP 1194
Ourapteryx sambucaria* LEP 1195
Lacosoma chiridota* LEP 1196
Orygia leucostigma* LEP 1213
Automeris io* LEP 1201
Dolba hylocus* LEP 1209
Schizura concinna* LEP 1212
Pseudaletia unipuncta* LEP 1226
Malacosoma americana* LEP 1198
Dilina tiliae* LEP 1208
Acherontia atropos* LEP 1205
Hepialus humuli* LEP 1108
Coptodisca splendoriferella* LEP 1117
Paraleucoptera sinuella* LEP 1126
Paraclemensia acerifoliella* LEP 1114
Prodoxus quinquepunctella* LEP 1116
Tischeria marginea* LEP 1113
Ithome concolorella* LEP 1135
Megaxyela* sp. HYM1230
Trichiosoma sorbi* HYM1237
Blasticotoma filiceti* HYM1246
Janus compressus* HYM1253
Pamphilius pallipes* HYM1234
Megalodontus spissicornis* HYM1232
Abia americana* HYM1235
Acordulecera* sp. HYM1247
Hoplocampa brevis* HYM1238
Arge macleayi* HYM1244
Diprion hercyniae* HYM1248
Dolerus similis* HYM1245
Pteronidea ribesii* HYM1241
Xiphydria camelus* HYM1249
Tremex columba* HYM1251
Cimbex americana* HYM1236
Pristiphora erichsonii* HYM1243
Neurotoma* sp. HYM1233
Sirex cyaneus* HYM1250
Ectoedemia heinrichi* LEP 1110
Nepticula malella* LEP 1111
Opostega* sp. LEP 1112
b

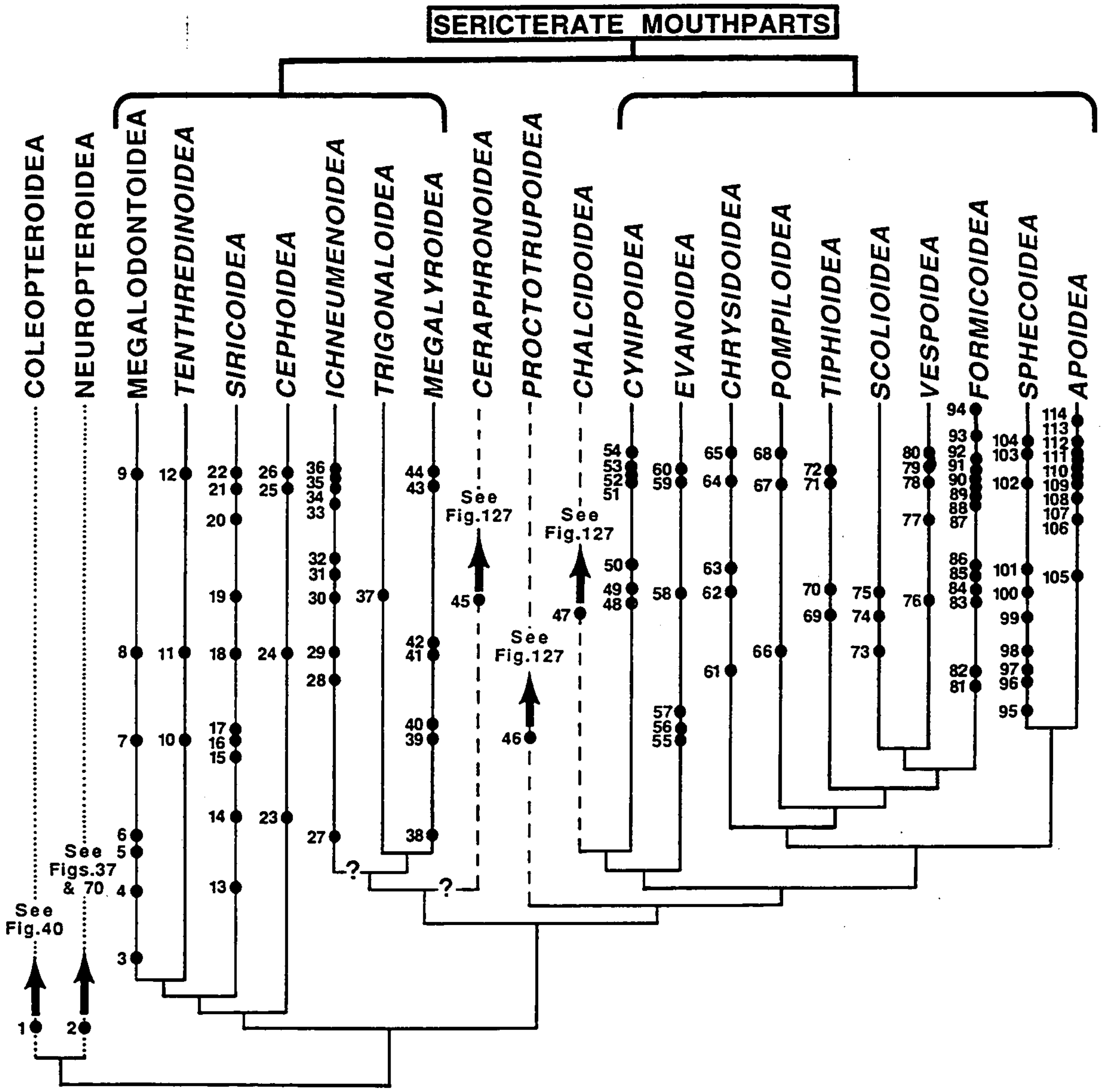

C
LEP 1097 Agathiphaga vitiensis*
HYM1254 Apanteles flavipes*
HYM1257 Bracon gelechiae*
HYM1259 Stenobracon dessae*
HYM1262 Xorides* sp.
HYM1258 Rhogas testaceous*
HYM1266 Evania appendigaster*
HYM1269 Aulacus striatus*
HYM1305 Elaphroptera erythrura*
HYM1260 Eulimneria crassifemur*
HYM1263 Agriotypus armatus*
HYM1267 Gasteruption assectator*
HYM1307 Mutilla lunulata*
HYM1328 Polistes gallicus*
HYM1310 Dipogon sayi*
HYM1312 Pseudagenica carbonaria*
HYM1311 Pepsis thisbe*
HYM1333 Ammophila campestris*
HYM1309 Rhopalosoma* sp.
HYM1321 Formica rufa*
HYM1300 Chrysis shanghaiensis*
HYM1332 Vespula sylvestris*
HYM1355 Anthophora stanfordiana*
HYM1360 Apis mellifera*
HYM1346 Andrena* sp.
HYM1351 Fidelia villosa*
HYM1358 Xylocopa virginica*
HYM1364 Trigona cupira*
HYM1361 Bombus americanorum*
HYM1313 Aphaenogaster subterranea*
HYM1316 Camponotus vagus*
HYM1327 Eumenes unguiculus*
HYM1284 Nasonia vitripennis*
HYM1285 Stenomalus liparae*
HYM1348 Protoxaea gloriosa*
HYM1252 Orussus occidentalis*
HYM1261 Pimpla nucum*
HYM1296 Ibalia leucospoides*
HYM1298 Rhodites rosae*

SERICTERATE MOUTHPARTS

Subcluster 1 consists of a diverse assemblage of 30 taxa of ditrysan lepidopterans (bracketed by data-set nos. 1089 to 1154 of Fig. 66) that are dominately large, external foliage feeders with prominent heads and hypognathous mouthparts. An exception to this theme is the distantly associated *Heterobathmia pseuderiacrania* which is a leaf-miner on the southern beech *Nothofagus*. The members of this theme are ectophagous feeders principally on leaves, stems and reproductive structures. Subcluster 2 (taxa 1108 to 1116) comprises five small forms that mine leaves and bore roots from the families Hepialidae, Incurvariidae, Opostegidae and Lyonettidae. These taxa are small, endophagous feeders with wedge-shaped heads and prognathous mouthparts. Subcluster 3 consists of two, small, leaf-mining genera from the Tischeriidae (1113) and Momphidae (1135) that have some unique mouthpart specializations. Subcluster 4 is a diverse suite of symphytan hymenopterans that are nestled between the leaf-mining subclusters 3 and 5. Members of this group are dominately external foliage-feeding forms and externally resemble the lepidopterous caterpillars of Subcluster 1. A few stem-miners also occur in this subcluster. Finally, Subcluster 6 consists of 39, apodous, maggot-like larvae (taxa 1097 to 1298). These taxa are either (i) endoparasitic or ectoparasitic on land arthropods, or (ii) are altricial larvae of solitary, subsocial or social wasps or bees that are fed by adults from the regurgitation of pollen, nectar or honey or by nest provisioning of dead or paralyzed arthropod prey. This cluster is frequently characterized by some head and mouthpart reduction, but not to the degree that typifies the parasitican hymenopteran larvae of the reduced-trophic mouthpart class (Section 8.10.2).

Geochronologic History. Two basic approaches are available for assessing the fossil history of sericterates. The first approach uses the body-fossil record (Fig. 67) and the second takes advantage of the unique trace-fossil record of external foliage feeding, leaf-mining and plant galls. Although both approaches present disadvantages, they nevertheless complement each other since they independently reflect the presence of imagines and larvae for the same mouthpart class in the fossil record.

The early history of sericterates probably evolved in parallel to that of mandibulobrustiates since trichopterans and lepidopterans are sister-groups (Kristensen 1975, 1981, 1984a; Hennig 1981) and it is not known when the stem-group to both taxa differentiated into one group with aquatic larvae (Trichoptera, mandibulobrustiates) and another group with terrestrial larvae (Lepidoptera, sericterates) (Whalley 1978). Direct evidence does not help since the earliest larval trichopterans are caddis cases of the Lower Cretaceous [53,52] (Sukacheva 1982, Jell and Duncan 1986) and the earliest caterpillars are Upper Cretaceous [35] (Mackay 1970, Skalski 1979, Whalley 1986). The indirect evidence of adult fossils, mostly wings, is more plentiful in lower Mesozoic deposits, although their ordinal assignment is fraught with difficulties since demonstrable constitutive apomorphies are absent (Hennig 1981). For this reason the twofold approach of determining the fossil record of sericterates from both body fossils and trace fossils is used. I will consider first the body fossil evidence.


SERICTERATE MOUTHPARTS
COLEOPTEROIDEA
NEUROPTEROIDEA
MEGALODONTOIDEA
TENTHREDINOIDEA
SIRICOIDEA
CEPHOIDEA
ICHNEUMENOIDEA
TRIGONALOIDEA
MEGALYROIDEA
CERAPHRONOIDEA
PROCTOTRUPOIDEA
CHALCIDOIDEA
CYNIPOIDEA
EVANOIDEA
CHRYSIDOIDEA
POMPILOIDEA
TIPHIOIDEA
SCOLIOIDEA
VESPOIDEA
FORMICOIDEA
SPHECOIDEA
APOIDEA
See Fig.40
See Figs.37 & 70
See Fig.127
See Fig.127
See Fig.127
?
?
1
2
3 4 5 6 7 8 9
10 11 12
13 14 15 16 17 18 19 20 21 22
23 24 25 26
27 28 29 30 31 32 33 34 35 36
37
38 39 40 41 42 43 44
45
46
47
48 49 50 51 52 53 54
55 56 57 58 59 60
61 62 63 64 65
66 67 68
69 70 71 72
73 74 75
76 77 78 79 80
81 82 83 84 85 86 87 88 89 90 91 92 93 94
95 96 97 98 99 100 101 102 103 104
105 106 107 108 109 110 111 112 113 114

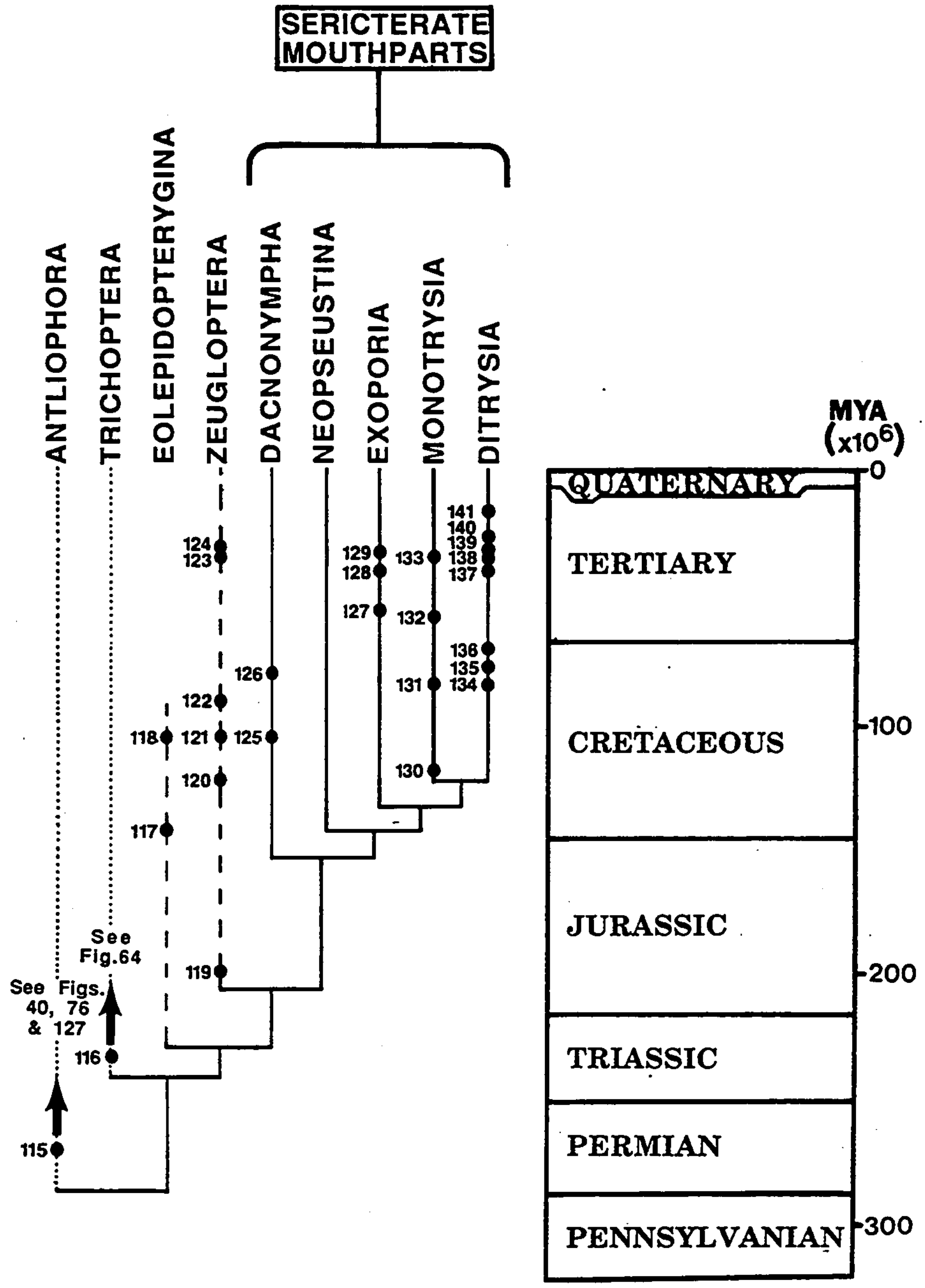


FIGURE 67. Geochronologic history of the Sericterate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Schlee (1970), Königsmann (1977, 1978a, 1978b), Rasnitsyn (1969, 1975), Kristensen (1981, 1984a) and Jamieson (1987). The taxonomic level of analysis is the superfamily for Hymenoptera and the suborder for Lepidoptera. The outgroups are Coleopteroidea and Trichoptera. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.

Two body fossils from the Late Triassic of Queensland [79], *Eoses* Eoses triassica Tindale 1945 and *Eocorona iani* Tindale 1980 presumably represent the earliest known lepidopterans (Tindale 1945, 1980). However all subsequent examinations of these fossils discount lepidopterous affinities (Skalski 1979, Whalley 1986, Shields 1988), although some authors provisionally assign them to the stem-group of the Trichoptera + Lepidoptera, the Amphiesmenoptera (e.g. Whalley [1986] for *E. iani*). Although the enigmatic Paratrichoptera also have been considered a subordinate taxon of the Lepidoptera (Riek 1976), the lack of constitutive characters disallows placement in the Lepidoptera (Hennig 1981, Whalley 1986). Also, nothing is known of larval paratrichopterans.

The earliest assured lepidopteran and thus body fossil evidence for the presence of the sericterate mouthpart class is *Archaeolepis* Whalley 1985 from the Lower Jurassic of England [69] and *Eolepidopterix jurassica* Rasnitsyn 1983 from the Upper Jurassic (stage unspecified) of the USSR (Whalley 1986). These forms precede the appearance of angiosperm plants during the Lower Cretaceous (Whalley 1985), implying that the highly coevolved relationship between modern sericterates and flowering plants was not an essential prerequisite for coevolution. Notably these Jurassic and many Cretaceous lepidopterans are zeuglopteran or zeuglopteran-like in affinities, and Recent larval zeuglopterans are known to feed on several nonangiospermous hosts (Tillyard 1922, Powell 1980, Kristensen 1984a).

In Lower Cretaceous amber from Lebanon [55] Whalley (1977, 1978) described incurvariid scales, the earliest occurrence of a proboscate lepidopteran, as well as a well-preserved micropterygid moth, *Parasabatinca aftimacrai* Whalley 1978. From Upper Cretaceous amber of northwest France [45], isolated micropterygid-like scales have been described (Küne et al. 1973, Schlüter 1974). Younger Cretaceous amber from Siberia [37] includes five lepidopterous specimens, including three homoneurous moths, one which is near the extant Lophocoronidae, an incurvariid moth and the earliest known caterpillar and hence sericterate (Zherikin and Sukacheva 1973, Skalski 1979, Whalley 1986). A better-preserved caterpillar, probably a tineoid, has been documented by Mackay (1970) from somewhat younger Canadian amber [35] (Whalley 1977, 1986). The controversial *Undopteryx sukatscheviae* Skalski 1979 from the Lower Cretacous of the USSR [31] may be a zeuglopterous lepidopteran, although Kristensen (1984a) considered it *incertae sedis*.

Numerous families of advanced ditrisan moths occur in Late Eocene/ Early Oligocene Baltic amber [19] (Rebel 1934, Skalski 1976, Kozlov 1988). The earliest advanced ditrysan groups, notably butterflies, are of a similar age (Durden and Ross 1978) and are found principally in the Early Oligocene of Colorado [15] (Scudder 1889, Cockerell 1913, Brain 1976). Direct evidence of the sericterate class during the middle Tertiary are caterpillars from the Eocene of England [26] (Rundle and Cooper 1971), the Upper Eocene/Lower Oligocene of England [18] (Jarzembowski 1980) and from the Upper Miocene of Germany [7] (Zeuner 1927, 1929).

The body fossil evidence suggests that the first indirectly documented appearance of the sericterate mouthpart class is Early Jurassic, although a substantial earlier history is implicated. Direct evidence demonstrates the presence of caterpillars during the Late Cretaceous. By Cretaceous time many monotrysan and ditrysan moths were present, but evidence for butterflies does not antedate the Eocene/Oligocene boundary.

A more direct and probably reliable expression of sericterate presence in the fossil record comes from observations of characteristic insect damage to plant organs, especially leaves and stems. Although the association of adults with presumed larval stages involves an assumption regarding the parallel evolution of adult and larva through time and the application of an actualistic approach, documentation of the direct damage of a plant by its insect herbivore can be a separate, independent method of establishing presence of the sericterate class. However, this approach must be tempered by recognition that specific patterns of sericterate leaf chewing, leaf-mining and galling can be recognized in the fossil record and be assignable to a characterizable extant sericterate taxon (after Crane and Jarzembowski 1980). There are three types of insect/plant damage that are relevant in documenting sericterates in the fossil record: external feeding traces, leaf-mining and galls.

The earliest presumptive evidence for externally-chewed leaves comes from Pennsylvanian-age coal floras. In the Mazon Creek flora of Illinois various chewing damage by herbivores that are assignable to probable orthopteroid or holometabolous insects have been described (Labandeira and Beall 1990, Beall and Labandeira, in prep.). In other Carboniferous floras several genera of pteridosperm fronds exhibit scalloped margins with thickened ridges bordering the bite mark (Van Amerom 1966, Van Amerom and Boersma 1971, Müller 1982, Scott and Taylor 1983, Labandeira and Beall 1990). Plumstead (1963) and Müller (1982) and Srivastava (1987) have described similar leaf damage of a Permian *Glossopteris* flora from South Africa, Germany and India, respectively. From the Middle Jurassic Yorkshire flora of England [63] Scott and Patterson (1984) have illustrated nibbled cycad leaves. Notably, in these Upper Paleozoic and Middle Mesozoic examples of external foliage feeding, there is no direct evidence indication predation by members of the sericterate class. A more parsimonious interpretation is that this foliage was chewed by adult-ectognathates, particularly orthopteroids and possibly coleopterans, whose presence is supported by body fossils of the same interval (Section 8.3.4). Occurrences of external sericterate damage in Cretaceous and younger floras (Brooks 1955, Scott and Patterson 1984) may be of sericterate origin.

The leaf-mining fossil record is better documented and post-Jurassic examples possess features that are diagnostic of modern leaf-mining sericterate families (Opler 1973, Crane and Jarzembowski 1980, Strong et al. 1984). Evidence exists for both blotch and meandering types of pteridosperm leaf-mining during the Pennsylvanian and Permian, particularly for European *Neuropteris*, *Callipteris* and *Odontopteris* (Potonié 1921, Müller 1982; but see Hering [1951] for a cynical view). This indicates the probable presence of holometabolous larval mining as early as the Pennsylvanian (Labandeira and Beall 1990, Beall and Labandeira, in prep.). Carnian-age Triassic leaf mines in ginkoacean and voltiacean conifers from Queensland, Australia have been described by Tillyard (1922), Rozefelds (1985) and Rozefelds and Sobbe (1987), although none of the evidence used to distinguish the ordinal affiliation of the leaf-miner (Strong et al. 1984) are present. Various nepticulid leaf-mines have been reported from Turonian-age Lower Cretaceous strata of the USSR [39] (Skalski 1979, Shields 1988, Kozlov 1988). More geologically recent leaf-mines include probable tineid mines on "*Aralia*" from the Cretaceous (stage unspecified) of Czechoslovakia (Fritsch 1882, Fric 1901) and unfigured and unnamed presumptive tineid and tortricid leaf-mines on Upper Cretaceous leaves of the Dakota Formation of Kansas and Nebraska (Hagen 1882).

Examples of Cenozoic leaf-mining are more plentiful. the oldest are three types of leaf-mines, two of which are assignable to the Nepticulidae, from the Upper Paleocene of southern England [29] (Crane and Jarzembowski 1980). Eocene deposits include nepticulid mines from Tennessee [25] (Brooks 1955, Opler 1973), a nepticulid *gangmine* resembling *Stigmella* from central Germany [24] (Straus 1976), and "probable lepidopteran" leaf-mines on dicotyledenous leaves in Eocene coals from Victoria, Australia (Rozefelds 1985). From Oligocene strata a possible nepticulid leaf-mine has been described from Germany by Heyden (1862), although it is considered dipteran by Opler (1973). From Miocene deposits Kvacek and Walther (1974) have figured a serpentine leaf-mine on *Daphnogene* (Lauraceae) from Germany and Opler (1973) has documented several occurrences of western North American, late Tertiary leaf mines of eriocraniids, nepticulids and lyonettids (see also Lewis 1969) and possibly gelechids, virtually all of which are associated with the Fagaceae, especially *Quercus* (oak). In that study Opler reviews previous accounts of Tertiary leaf-mines and suggests that because these leaf-mines are structurally indistinguishable from Recent conspecific leaf-mines, these specific insect-host relationships extend at least to the Miocene.

The plant gall record is less abundant than the leaf-mining record. Two dubious occurrences have been described in strata predating the first appearance of angiosperms--namely a gall-like structure in a stigmarian rootlet (Weiss 1904) and pustulose structures on a pinnule from a Carnian-age Triassic dipteridacean fern from southeastern Queensland [74] (Webb 1982). These structures are more properly assigned to a fungal gall and to insect eggs, respectively. The earliest assured galls are 49 cynipid-like structures on Early Cretaceous platanalean leaves of "*Sassafras*" (Larew 1986), described by Doyle and Hickey (1977). This occurrence [49] is important since most extant sericterate galls are caused by cynipid wasps, which exclusively gall the Fagaceae, especially *Quercus* (Frost 1959). Brooks (1955) has figured and discussed mamilliform galls on *Nectandra* (Lauraceae) from the Eocene of Tennessee [25], possibly of cynipid origin. Hoffman (1932) discussed cynipid galls on an Upper Miocene *Quercus* leaf from Douglas Canyon, Washington. These occurrences, together with Straus' (1977) documentation of three cynipid galls in Pliocene deposits of Germany and the presence of modern-aspect cynipid adults during the

Eocene (Kinsey 1919, Keilbach 1982), indicate that the cynipid/oak gall relationship also extends at least to the Miocene.

These and other data indicate that by Late Paleozoic time and certainly by the end of the Permian, insect feeding directly on plants was present--a conclusion also supported by Rohdendorf and Rasnitsyn (1980), Southwood (1984) and Owen and Wiegert (1987). Nevertheless, whereas external folivory by chewing extends to the Late Paleozoic, probably to the Pennsylvanian, the identity of the culprit is not certain and is more plausibly an orthopteroid rather than holometabolous larvae. The occurrence of sericterate style external foliage-feeding is not abundant until the Jurassic. Also, leaf-mining apparently appeared early (Müller 1982, Labandeira and Beall 1990), during the Pennsylvanian, although it is not certain whether any taxon in the sericterate mouthpart class was the responsible agent. I am considering the culprits of these Paleozoic occurrences as a holometabolous group other than sericterates and undoubtedly extinct. Good evidence for the leaf-mining feeding habit of modern aspect is present during the Triassic and unequivocal evidence commences during the Late Cretaceous to the Recent. Although plant galls lack a significant pre-Cretaceous fossil record, they are probably the most recently evolved of the three dominant sericterate feeding modes. (Some of these views are contrary to those of Strong et al. [1984], Fig. 2.13.) The presence of leaf-mining and plant-galling only in advanced holometabolous groups (Jolivet 1986) may be a fundamental reason for the difficulty of documenting these feeding modes until Late Mesozoic floras appear. This fact does not explan the rarity of both feeding modes until the Cretaceous, unless intimate angiosperm/holometabolous-insect coevolution is invoked as the causative factor. Notably, leaf-mining members of the sericterate class are coevolved with nonangiospermous vascular plants and thus an Early to Middle Mesozoic (or even earlier?) existence should not be surprising.

Previous Designations. Mouthparts herein described as sericterate previously have been termed as mandibulate (Metcalf 1929, Metcalf et al. 1962, Ross et al. 1982). Metcalf (1929: 112) classified larval lepidopteran and similar larval hymenopteran mouthparts as "the chewing type" of his Mandibulate Series, a categorization paralleling Metcalf et al. (1962: 140-141) designation of a "grinding or masticatory subtype" of their Chewing Type (Table 6). Traditionally, the notion of "generalized mandibulate mouthparts" has included principally nymphal and adult orthopteroids, adult neuropteroids, adult coleopterans and most holometabolous larvae, all of which chew on predominately solid food (e.g. Chaudonneret 1982). However, this assemblage contains considerable structural variation and most holometabolous larvae bear head structures and downscaled or highly modified mouthparts that significantly depart from the orthopteroid or coleopterid mandibulate standard (Snodgrass 1928, 1935).

Since the taxa comprising the sericterate mouthpart class constitute a large and discrete cluster (Fig. 28), they are separable from the "typical" mandibulate mouthparts of adult-ectognathates and larval-ectognathates (Sections 8.3.4 and 8.3.5). A characteristic, recognizable feature of this group is the spinneret, or silk press, of the labiohypopharyngeal region (although it is also present in mandibulobrustiates), to which the name, "sericterate" refers (Greek: *serici-*, silk or silken). Although the term "sericterium" is a generalized name for the silk-spinning apparatus of caterpillars (Torre-Bueno 1985) and even hymenopterous parasites (Gurney 1953: 26), the designation sericterate is new and has no prior history.

Review of Literature. The sericterate mouthpart class is abundantly documented, particularly in several taxonomic monographs. This documentation is attributable to the sheer abundance and diversity of sericterates, some of which are important consumers of agricultural crops worldwide and in most instances by their relatively large size, which allows for relatively facile dissections. An additional incentive for documentation is the use of head characters, particularly setation, as a diagnostic criterion for identification at lower taxonomic levels. This discussion will divide the sericterate literature into (i) monographic accounts of larger taxonomic groups, (ii) comprehensive head and mouthpart descriptions of one or a few species and (iii) studies of particular mouthpart or head structures, usually for two or more species.

Monographic documentation of sericterate mouthparts and head structure includes (i) studies based on economically-important groups, (ii) studies focusing on descriptions of species from particular families or superfamilies and (iii) general surveys of lepidopterans and hymenopterans from descriptions of selected representative species. Surveys of economically important groups include Hinton (1943) for lepidopterans associated with stored grain and Hinton (1957) on pestiferous tineids. Leaf-mining froms from many families, some of commercial importance, were described by Trägardh (1913) and Jayewickreme (1940). Major taxonomic treatments include Ripley (1923) and Crumb (1956) for noctuids, Evans (1959) for pamphilids, and Yuasa (1922) and Lorenz and Kraus (1957) for tenthredinoids and megalodontoids. General, nontaxonomic surveys of lepidopterans and hymenopterans include Mackay (1972) for North American microlepidopterans, Forbes (1910, 1911) for lepidopterans in general, Short (1952) for hymenopterans in general, and Peterson (1948) for excellent line drawings and life-history descriptions of dominately herbivorous lepidopterans and hymenopterans.

More narrowly-focused studies describing head and mouthpart structures of individual species include, for microlepidopterans, Dumbleton's (1952) discovery of the agathiphagid *Agathiphaga vitiensis* Dumbleton; Briolini's (1960) account of the nepticulids *Nepticula stigmella* Stainton and *N. pomonella* Vaughn; Heinreich's (1918) comparative study of the opostegid *Opostega* sp., the nepticulid *Ectoedema phelophaga* Busck, the tischeriid *Tischeria quercivorous* Chambers and the leucopterygid *Proleucoptera albella* Chambers (see also Briolini 1965); Randriamomonjy's (1963) description of the gelechid *Phthorimaea* Loew; Lopez's (1929) study of the tortricid *Cydia pomonella* (Linneaus); Ippolito's (1977) study of the tortricid *Cnephasia incertara* Trägardh and *C. cinereana* Chrystal; and Silvestri's account and life-cycle description of the tortricid *Tortrix viridana* Linneaus. Descriptions of macrolepidopterous larval head and mouthpart structure include Grandi's (1924a) classical account of the bombycid *Bombyx mori* Linneaus, Peterson's (1912) study of the arctiid *Pyrrharctia isabella* (Smith and

Abbott), and Dyar's (1896) brief description of the agaristid *Agrotis* sp. Descriptions of hymenopterous sericterates include Arora's (1959) examination of the diprionid *Diprion pini* Linneaus, Bird's (1927) examination of the tenthredinid *Hoplocampa halcyon* Norton, and Wong's (1963) description of the tenthredinid *Pristiphora erichsoni* (Hartig).

Detailed examinations of particular head or mouthpart elements, often for an ensemble of species, involved light microscopy in earlier works and scanning electron microscopy in modern studies. Representative examples of the former include Dethier (1937) and DuPorte (1956) for internal head structures of *Manduca quinquemaculata* (Haworth), Hasenfuss (1969) for the taxonomic importance of head setation in monotrysan and ditrysan larvae, Middleton (1917) for a brief description of the antennae and selected mouthparts of four genera of cephid larvae, Hinton (1947) for a description of the dorsal cranial area, particularly the frontoclypeus, of several lepidopteran species, DeGryse (1915) for documentation of modifications of the hypopharynx and associated structures among lepidopterans, and Djamin and Pathak (1967) for the role of silica in dental wear of the mandibles of *Chilo supressalis* (Walker). Examples of the latter include Grimes and Neunzig (1986a, 1986b) who used scanning electron microscopy for documentation of maxillary and mesal lobe structure among representatives from most superfamilies of ditrysan lepidopterans.

8.4. Mandibulo-Canaliculate Series

8.4.1. General Features of the Mandibulo-Canaliculate Series

General Structure. Mandibulo-canaliculate mouthparts are characterized by a prominent pair of widely-spaced, scythe-shaped mandibles or mandible analogs, each which bears a duct or channel that opens terminally and debouches into a mouth located at the base of the mandibles. These mostly edentate, tissue-piercing structures are represented by three types: (i) a structure with a mandible and a superposing articulating lacinia forming the tube when engaged, (ii) a simple tubulate mandible and (iii) a mouthhook that generally bears a longitudinal tubule and articulates to various basal, maxillary sclerites. The plane of mandibulate adduction/abduction is transverse in the former two and parasagittal in the latter. The labium and maxillary palpi are highly reduced and often externally absent. The sucking pump is cibarial or esophageal. Co-opted mouthpart elements are present, namely a mandible/lacinial complex in the Fossate Complex Class and a modified cephalopharyngeal complex in the Mouthhook Class. The head is frequently dorsoventrally flattened, without compound eyes and usually without ocelli.

The key feature of the Mandibulo-Canaliculate Series is a falcate mandible or a mandible-analog used as a syringe for piercing tissue. This structure is used initially for injection of lytic enzymes for fluidizing tissues of prey items (dominantly insects) and then for extraction of the fluid prey contents. This structure is connected near-exclusively with fluid-feeding, although some members of the

Mouthhook Class ingest suspended particulate material in their fluid-feeding, which they pharyngeally filter.

Included Classes. The Mandibulo-Canaliculate Series consists of the Fossate Complex, Tubulomandibulate and Mouthhook Mouthpart Classes. (See Table 5 for taxal membership, life-stages and number of taxa examined for each mouthpart class).

Diversity and Other Distributional Patterns. Mouthparts of the Mandibulo-Canaliculate Series occur only in predaceous, holometabolous larvae feeding by fluid ingestion. Mandibulo-canaliculate mouthparts have been a successful, but taxonomically limited, strategy for aquatic and terrestrial entomophages (although some members of the Mouthhook Class are parasitoids). Whereas the Fossate Class has originated once in the Planipennia and the Mouthhook Class has presumably originated once among the brachycerous Diptera (see Henning 1953, 1981 for brachyceran monophyly), the Tubulomandibulate Class has minimally three independent origins in the Coleoptera--once among the Hydadephaga and twice among the Cantharoidea. Other, more diverse, larval coleopteran groups--the vast majority of predaceous forms--have retained larval-ectognathate mouthparts (see Section 8.3.5). In terms of insectan taxonomic diversity, when compared to other mouthpart series, mandibulo-canaliculate mouthparts have not proved to be a widespread mode of feeding. Although the independent origin of mandibulo-canaliculate mouthparts has resulted from at least five evolutionary lineages, this convergence has not guaranteed the high taxonomic diversity observed in other mouthpart series with less convergence.

Major Structural Variations. All three classes of the Mandibulo-Canaliculate Series represent unique structural solutions for mandibulate larvae engaged in (i) injection of lytic secretions into prey by a mandible or mandible analog and (ii) uptake of fluidized prey contents while using the same mandible like structure. The simplest mechanism occurs in the Tubulomandibulate Class, where duct-bearing mandibles are associated with minimal modification of the head capsule and mouthparts. Rather than possessing a closed tube oriented lengthwise through the mandible, the Fossate Class also bears a falcate mandible but with an upper, longitudinally positioned gutter that is enclosed by a similarly-shaped lacinia that fits over the mandibular gutter. When the mandible and lacinia are apposed, a tube results for discharge or uptake of fluid materials. Finally, in the Mouthhook Class, mouthhooks superficially resemble tubulate mandibles but are articulated to a complex of intermediary maxillary sclerites for efficient abduction and clinging to prey items or hosts. The diversity of mouthpart structure among these three classes contrasts to an overall similarity in feeding mode and diet.

Geochronologic Range. The earliest occurrence of the Mandibulo-canaliculate Series was the Fossate Class, which is traceable by indirect association with planipennian wings to the Artinskian Stage of the Lower Permian [90]. These wings represent members of the superfamilies Ithonoidea and Hemerobioidea (Crowson et al. 1967). The earliest tubulomandibulate and mouthhook mouthparts occurred later, during the middle Mesozoic (*vide infra*).

8.4.2. Fossate-Complex Class
(Class 13)

Description. Head spheroidal to rarely anteriorly prolonged, exserted from the thorax; proboscis short; head nonretractile. Genae expanded laterally comprising most of the cranium; gula mostly absent (replaced by prementum) or well-developed. Antennae long, filiform; stemmata two or numerous, or absent; compound eyes absent. Mouthparts mandibulosuctorial, prognathous, symmetrical, nonretractile. Food pump clypeal and pharyngeal.

Clypeus quadrate or transversely elongate; fused to labrum; occasionally absent. Labrum variously shaped; of one segment or part of clypeolabrum; margin mostly straight to curvilinear, or apertuate. Food canal narrow; hypopharynx lobate, adjoined to labrum, or a brace for mouthparts; epipharynx membranous. Mandibles dicondylic; grooved and falcate; dentition with an incisiform region, or hamate, or edentate; musculation with adduction/abduction normal to sagittal body plane. Maxilla composed of 2 variously shaped, basal sclerites of main-body; bearing a lacinia only. Maxillary palps and galeae absent. Each mandible/maxillary pair forms a complimentary interlocking structure bearing a longitudinal gutter serving as a tube for fluid food. Labium with main-body of two elongated sclerites; bearing labial palpi only. Labial palpi filiform; 2- or 3-segmented, rarely 1- or 4-segmented; length long. Glossae and paraglossae absent. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. The dominant diagnostic character of the Fossate-Complex Class is the mandibulo-maxillary apparatus. Each mandible/lacinia unit is deployed as overlapping, interlocking, sickle-shaped blades that form a tubular food canal. Secondary features include a cranial capsule that is almost always dorsoventrally flattened, and significant mouthpart reduction, especially the absence of maxillary galeae and palps, and labial glossae and paraglossae.

Diversity and Natural History. The Fossate-Complex consists of the immature stages of planipennians, commonly known as antlions, lacewings and mantispids. Members of this class are larvae that are universally predaceous and fluid-feeding (Balduf 1939, Richards and Davies 1977) (Fig. 68). Collectively they consume a wide variety of insect prey. Several groups specialize on prey such as scarab larvae (ithonids), adult ants (myrmeleonids), spider eggs (mantispids), and homopterans and mites (chrysopids) (Hagen 1987). Most fossate-complex taxa are terrestrial, occurring in or on the ground; a few are aquatic, feeding on insect nymphs or sponges (Balduf 1939). Although constituting 17 families, 694 genera and 4,200 species, they only comprise a paltry 0.5% of all extant insects (Appendix D). This corresponds to a rank-order of 23 out of 34 mouthpart classes (Table 5, Fig. 131). Nevertheless, members of the fossate-complex are locally important as insect predators in or on sandy soils (myrmeleonids, nemopterids and ascalaphids), in forest litter or bark (psychopsids, conipterygids, osmylids, hemerobiids and chrysopids), or within various insect domiciles where they actively seek out prey (berothids) (Clausen 1940, Hagen 1987).

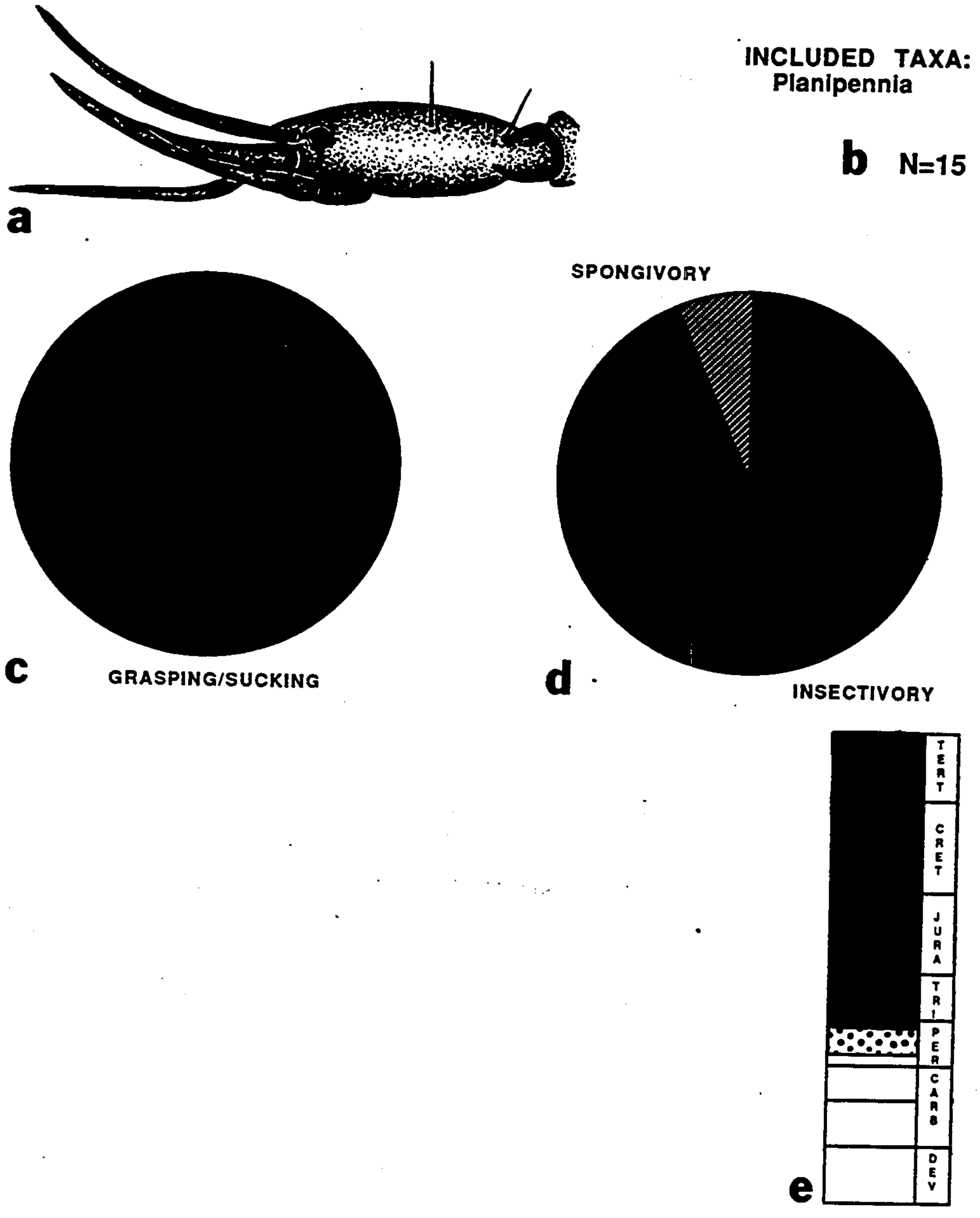


FIGURE 68. Overview of the Fossate Complex Mouthpart Class. a, *Neurorthus fallax* (Rambur) (Planipennia: Neurorthidae, data-set no. 377), after Zwick (1967); b, taxonomic distribution and number of taxa examined; c, functional-feeding-group; d, dietary spectrum; e, geochronologic range.

The fossate-complex procures prey either by active stalking or by passive waiting for the approach of a suitable victim. The latter habit is accomplished either by constructing a depression in sand for the entrapment of cursorial insects or by positioning the larva predator adjacent a food lure, such as a resin seep on a branch, and awaiting the approach of attracted prey. In all cases securing prey is effected by the rapid adduction of the mandibular/maxillary complex on the body of the prey, followed by active pumping of the victim's body fluids until the result is a shrivelled carcass.

Structural Themes. Mouthparts of the fossate-complex consist of four major themes, each of which is represented by a major subcluster in Fig. 69. Nine characters dominately contribute to the subdivision of the fossate-complex mouthparts, namely head shape, food pump type, labral participation in a multielement mouthpart structure, hypopharynx type, mandibular dentition, lacinial modification, type of labial appendages, and labial palpus type and aspect-ratio. Most of these characters involve special modifications of the mandibles and laciniae among various planipennian groups.

Two major subclusters occur among fossate-complex mouthparts. Subcluster 1 consists of coniopterygid and dilarid taxa (bracketed by data-set nos. 368 to 373 in Fig. 69). Larvae of Subcluster 1 generally bear abbreviated antennae and labial palps and relatively short, stout mandibles and laciniae. Subcluster 2 is more taxonomically diverse, consisting of the remaining superfamilies of Mantispoidea, Osmyloidea, Hemerobioidea and Myrmeleontoidea (data-set nos. 374 to 394) and are

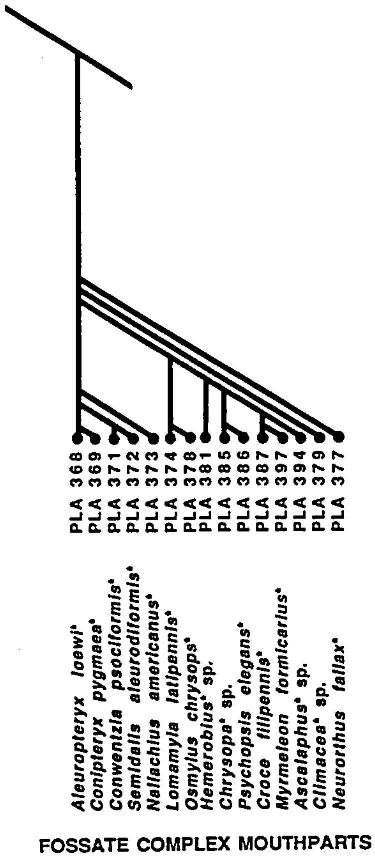

PLA 368 Aleuropteryx loewi*
PLA 369 Coniopteryx pygmaea*
PLA 371 Conwentzia psociformis*
PLA 372 Semidalis aleurodiformis*
PLA 373 Nallachius americanus*
PLA 374 Lomamyia latipennis*
PLA 378 Osmylus chrysops*
PLA 381 Hemerobius* sp.
PLA 385 Chrysopa* sp.
PLA 386 Psychopsis elegans*
PLA 387 Croce filipennis*
PLA 397 Myrmeleon formicarius*
PLA 394 Ascalaphus* sp.
PLA 379 Climacea* sp.
PLA 377 Neurorthus fallax*
FOSSATE COMPLEX MOUTHPARTS

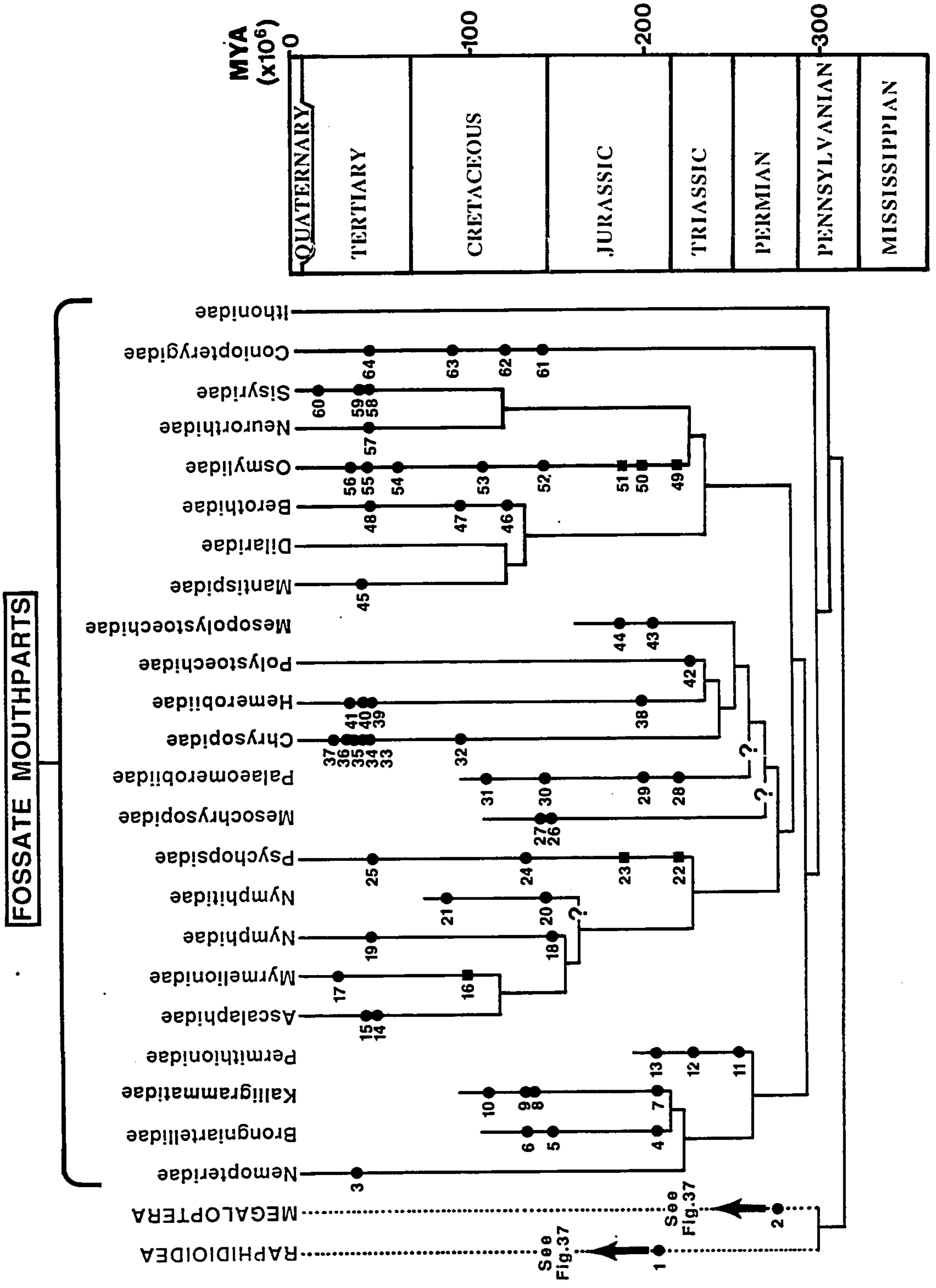
FIGURE 69. Cluster analysis dendrogram of taxa comprising the Fossate Complex Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

typified by long antennae and palpi, and elongate, falcate mandibles and laciniae. Subclusters 3 and 4 represent structurally isolated, aquatic taxa and respectively includes the sisyrid *Climacea* sp. (379), a spongivorous form, and the probably closely related (Zwick 1967) neurorthid *Neurorthus fallax* (378).

Geochronologic Range. Members of the fossate-complex originate from the presumably monophyletic group, Order Planipennia, which is one of three orders of the neuropteroid complex (=Neuroptera sensu lato) (Boudreaux 1987). Neuropteroids have a Late Paleozoic origin (Fig. 70) and it appears that megalopterans are more primitive than either raphidiopterans or planipennians (Hennig 1981). A larva of a megalopteran has been found in the Upper Permian of the Soviet Union [97] (Sharov 1953, Rasnitsyn 1977) and adult megalopteran wings occur in the Lower Permian of the Soviet Union [59] (Martynova 1961, Crowson et al. 1967).

Three major Permian fossil insect deposits--Elmo of the US [90], Chekarda of the USSR [89] and Belmont of Australia [83]--indicate the presence of the fossate-complex during the Late Paleozoic. Adult planipennians from the earliest of these deposits, the Wellington Formation of Kansas [90], have been described by Tillyard (1932, 1937) and Carpenter (1943) and consist of two genera of Permoberothidae. Although permoberothids are the oldest known planipennian family (Laurentiaux 1953, Carpenter 1954), including the Kansan taxa *Permoberotha villosa* Tillyard and *Permobiella perspicua* Tillyard, Tillyard (1937) and Carpenter (1954) state that the origin of planipenniams must

FIGURE 70. Geochronologic history of the Fossate Complex Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Withycombe (1924) modified by Hennig (1981), and Kristensen (1981). The taxonomic level of analysis is the family. The outgroup is Megaloptera + Raphidioptera. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.


MYA (x10⁶)
0
100
200
300
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
PENNSYLVANIAN
MISSISSIPPIAN
Ithonidae
Coniopterygidae
Sisyridae
Neurorthidae
Osmylidae
Berothidae
Dilaridae
Mantispidae
Mesopolystoechidae
Polystoechidae
Hemerobiidae
Chrysopidae
Palaeomerobiidae
Mesochrysopidae
Psychopsidae
Nymphitidae
Nymphidae
Myrmeliontidae
Ascalaphidae
Permithionidae
Kalligrammatidae
Brongniartellidae
Nemopteridae
MEGALOPTERA
RAPHIDIOIDEA
FOSSATE MOUTHPARTS
See Fig.37
See Fig.37
?
?
?
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64

have occurred during the Late Carboniferous, based on the relatively advanced structure of the Early Permian forms. In somewhat younger strata at Cherkarda [89] and Belmont [83], more diverse assemblages of planipennians have been documented (Martynov 1923; Tillyard 1926; Riek 1953; Ponomarenko, in Rohdendorf 1980), comprising minimally four families: the Palaeomerobiidae, Prohemerobiidae, Permithionidae and Permosisyridae. Although these families bear names suggesting relationships to modern planipennian families, their taxonomic identity may be less straightforward according to Carpenter (1954) who only recognizes two families, reassigning the other two to the related orders Caloneurodea and Glosselytrodea (MacLeod 1970).

During the early Mesozoic, deposits of Late Triassic age from Queensland, Australia [74] (Tillyard 1917, 1919, 1922, 1923) and Late Jurassic age from Mecklenburg and environs, Germany [68] (Handlirsch 1908, Bode 1953) have yield several genera, principally of the Prohemerobiidae and Psychopsidae. Although several extant families enter the fossil record during the Jurassic, including the Chrysopidae (Meunier 1898, Laurentiaux 1953), Psychopsidae (Hong 1983), Osmylidae (Ponomarenko 1984) and Coniopterygidae (Meinander 1975), several characteristic extinct Mesozoic planipennian families occur, including the Osmylitidae, Mesithonidae, Prohemerobiidae, Mesopolystoechitidae and the distinctive Kalligrammatidae, characterized by butterfly-like wings up to 25cm in total span (Laurentiaux 1953, Rohdendorf and Rasnitsyn 1980, Ponomarenko 1984, Whalley 1986, Lambkin 1988). These forms occur in deposits such as the Solenhofen lithographic limestone [61] (Hagen

1862, Carpenter 1929) and the Haiffanggou and Jiulongshan Formations of China [64] (Hong 1983). The first direct indication of fossate-complex mouthparts is a possible neuropteran from the Upper Jurassic of Britain [57?], specifically a "vermiform larva" which apparently has "a distinct head and sickle-shaped jaws" (Whalley and Jarzembowski 1985: 401), described by Brodie in 1845. Although adult neuropterans have recently been described or indicated in various Cretaceous ambers [45, 37] (Zherikin and Sukacheva 1973, Schlüter 1978), larvae have only been documented for the lower Tertiary Baltic Amber [19] (Kruger 1923, MacLeod 1970, Larsson 1978). These occurrences constitute the earliest direct evidence for the presence of the fossate-complex. Later Tertiary deposits, particularly at Florissant [15] (Cockerell 1908, Carpenter 1943), have yielded many adult planipennian fossils.

Previous Designations. Historically, fossate-complex mouthparts have been given a nomenclature indicating that they are essentially mandibulate mouthparts, with some suggestion that they comprise a unique functional solution for the imbibation of fluid food. Thus, they have been characterized as "the chewing type" of the Mandibulate Series by Metcalf (1929), the "grasping-sucking" or "mandibulo-suctorial type" of the "chewing type" by Metcalf et al. (1962) and "piercing and sucking" by Smith (1985) (see Table 6). Recently, Chaudonneret (1984) has referred to larval planipennian mouthparts as a distinct type of predatory mouthparts, labelling them as "*pièces buccales predatrices suceuses mandibulo-maxillaires.*" I have decided to use the strictly morphological term fossate-complex to refer to the unique condition of these mouthparts wherein a mandibular and maxillary gutter, or *fossa* (Latin: a ditch, trench, channel), is present on the prominent mandibles and laciniae of all members of the mouthpart class.

Review of Literature. Classical functional/morphological treatments of fossate-complex mouthparts are provided by Wundt (1961) for the osmylid *Osmylus chrysops* Linneaus, and Rousset (1966) who provided a detailed and comparative study of the conipterygids *Aleuropteryx loewi* Klapalek, *Coniopteryx pygmaea* Enderlien, *Conwentzia psociformis* (Curtis), *Semidalis aleurodiformis* (Stephens) and the chrysopid, *Chrysopa* sp. Genay (1953) has presented a less detailed survey of *Coniopteryx pygmaea*, *Osmylus chrysops* and the hemerobiid *Hemerobius nitidalus* Fabricius. Similarly Withycombe (1922) presented a synopsis of British larval planipennians, describing species of chrysopids, hemerobiids, sisyrids, osmylids and chrysopids, many of which are the same species mentioned by Genay (1954) and Rousset (1966). Additionally, Peterson (1951) figured several North American species.

More specialized accounts focusing on the structure of spingle species include Gurney (1947) for the dilarid *Nallachius americanus* (MacLachlan) and the berothid *Lomamyia* sp., Imms (1911) for the unusual *Croce filipennis* Westwood occurring in the tombs of Egyptian pyramids, Lozinski (1908) and Korn (1943) for the antlion *Myrmeleon europaeus* Linneaus, Principi (1954) for *Chrysopa viridana* Schneider, Tillyard (1923) for the ithonid *Ithone fusca* Newman, and Zwick (1967) for the neurorthid *Neurorthus fallax* (Rambur). A recent account by Griffiths (1980) has established associations between various behavioral, morphological and environmental variables and feeding success rate for the antlion *Morter obscurus* Rambur.

8.4.3. Tubulomandibulate Class
(Class 14)

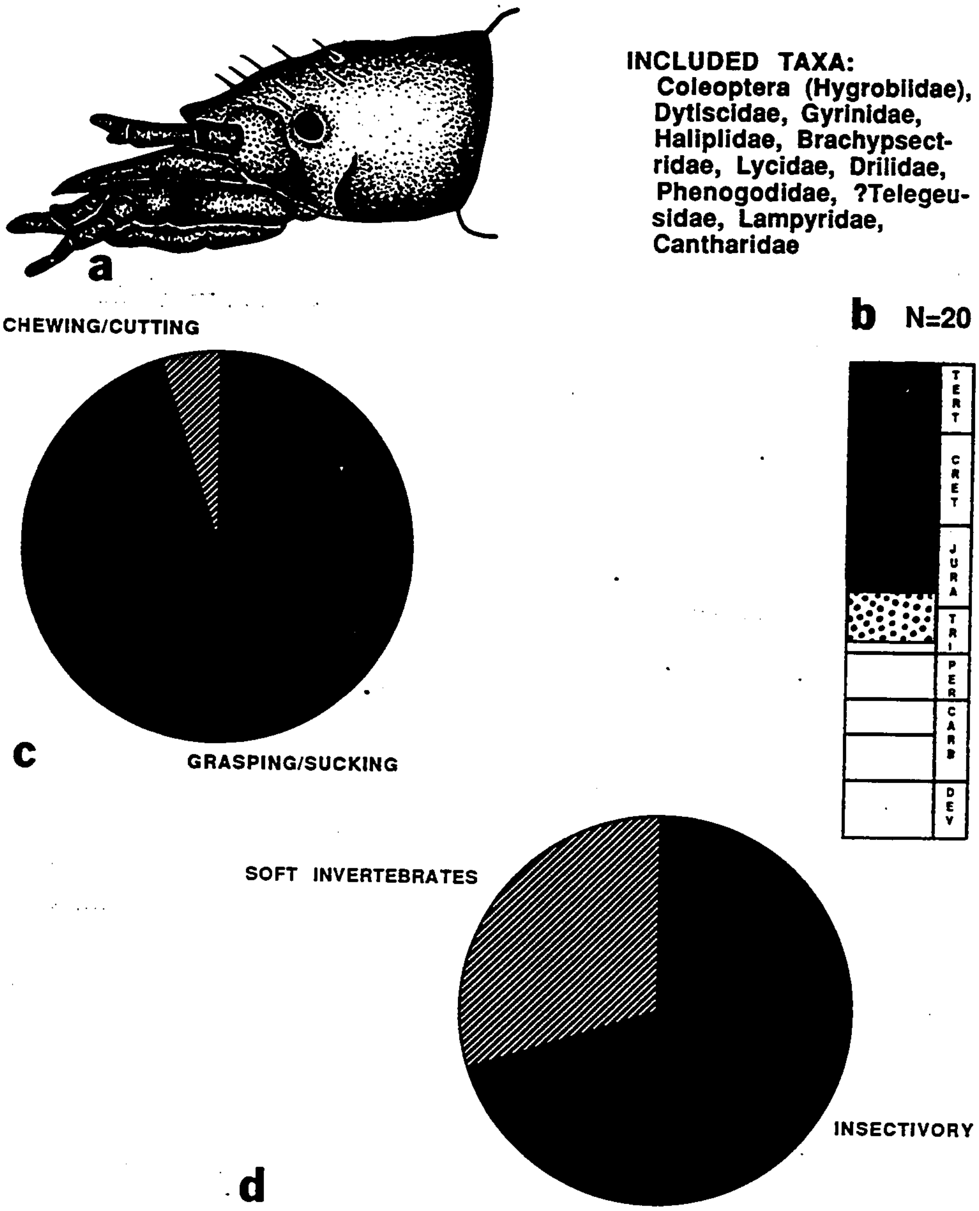
Description. Head spheroidal, nonproboscate, nonretractile; prothorax often enveloping posterior head capsule. Genae expanded dorsoventrally, comprising most of cranium; gula generally prominent and well-developed, infrequently minimally developed. Triangular fronto-clypeal sclerite delimited by an inverted Y-shaped suture. Antennae filiform, palpiform or stubby; stemmata 2 or supernumerary; compound eyes absent. Mouthparts mandibulosuctorial, prognathous or hypognathous, symmetrical and nonprotractile. Food pump variously developed.

Clypeus transversely elongate or quadrate; fused to frons; infrequently absent. Labrum with indistinct boundaries; fused to clypeus or rarely a nasale; margin various but often pectinate or acuminate; absent in some. Pharynx proper diminutive; hypopharynx lingulate and lobate or a bulbous reservoir with an apertuate lobe. Mandibles dicondylic; falcate, tubulate to rarely grooved; edentate; musculation of adduction/abduction. Maxillae with main-body of two sclerites; stipes equant to elongate; almost always bearing galea and palpi only, or palpi only. Maxillary palpi stubby, mucronate or filiform-clavate; 4- to 6-segmented; mostly short in length. Galea palpiform, long and cylindrical with a terminal setal tuft, or absent; laciniae absent to rarely present and mucronate. Labium equant to elongated with main-body of two sclerites; bearing labial palpi only.

Labial palpi filiform or mucronate to rarely papillate; 2- or 3-segmented; short or long in length. Glossae and paraglossae absent. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. The only distinctive feature of the Tubulomandibulate Class is the presence of falcate mandibles perforated by an internal food tube that are positioned laterally on the head capsule, adjacent the lateral cranial wall where the antennae are inserted. These mandibles are perpendicular to the sagittal axis, unlike the mandibles of the Mouthhook Class which articulate parallel to the sagittal axis. Like other holometabolous larvae, the maxillary and labial elements of tubulomandibulates are abbreviated.

Diversity and Natural History. The Tubulomandibulate Class is overwhelmingly characterized by predaceous and, less commonly, scavenging feeding habits; diets are typified by carnivory, particularly insectivory (Hagen 1987) (Fig. 71). They are found in two disjunct habitats: as nekton in the shallow aquatic zone in freshwater and as cursorial predators in forest litter, under bark or in decaying wood (Peterson 1951, White 1983, White et al. 1984). In both habitats, tubulomandibulates are important primary predators, even though as a mouthpart class they comprise 12 families, 567 genera and 14,487 species of larval coleopterans (Appendix D). This translates to a rank-order of 14 out of 34 mouthpart classes (Table 5, Fig. 131). However, they do represent the independent acquisition of a specialized mode of mandibulate fluid-feeding in one lineage of Hydadephaga and at least two lineages of Cantharoidea (Crowson 1972, 1981; Lawrence and Newton 1982).



INCLUDED TAXA:
Coleoptera (Hygrobiidae), Dytiscidae, Gyrinidae, Haliplidae, Brachypsectridae, Lycidae, Drilidae, Phenogodidae, ?Telegeusidae, Lampyridae, Cantharidae

FIGURE 71. Overview of the Tubulomandibulate Mouthpart Class. a, *Chauliognathus* sp. (Coleoptera: Cantharidae, data-set no. 576), after Peterson (1951); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

The superfamily Hydadephaga comprises six families of adephagan beetles, generally associated with freshwater and rarely marine habitats. Of those, at least four families, the Haliplidae, Hygrobiidae, Dytiscidae and Gyrinidae, have larval stages that bear specialized tubulate mandibles. The dominant taxon among the four is the Dytiscidae (predaceous diving beetles) who are eclectic predators on aquatic insects, molluscs, earthworms, tadpoles and small fish (White 1983) and the Gyrinidae (whirligig beetles) who are predators and scavengers on dead insects in the neuston zone (White et al. 1984). The nondiverse Hygrobiidae is a small family whose aquatic larvae consume worms and torpid larvae of insects (Clausen 1940). The Haliplidae (crawling water beetles) is the only major exception to the general feeding pattern in the class, since they feed on submerged herbaceous material. Although the adult stages of all four hydradephagan families are aquatic, members nevertheless are capable of emerging from water and pupating (Crowson 1981).

The Cantharoidea, a superfamily of elateriform polyphagan beetles (Lawrence and Newton 1982), contains at least four families with larval tubulomandibulate mouthparts. Virtually all of the species in these families are predaceous and carnivorous in feeding habits (Crowson 1981) and most exhibit bioluminescense at some or all stages of their life cycle (Clausen 1940). These forms are terrestrial, often occurring in damp conditions in forest litter and similar habitats. The most diverse family, the Cantharidae (soldier beetles), have flattened larvae that consume soft-bodied invertebrates, including insect larvae, invertebrate eggs and nonsclerotized insects (Clausen 1940, White 1983). The cylindrical larvae of the Lampyridae (lightningbugs, fireflies) also consume soft-bodied invertebrates but prefer snails and slugs (Clausen 1940, Brues 1972). The less known Phenogodidae (glowworms) are also litter-dwelling forms and feed on soft-bodied insects (White 1983) or on millipedes (Richards and Davies 1977). Finally, larvae of the non-diverse Brachypsectridae (Texas beetles), tentatively placed in the Cantharoidea (Lawrence 1987), feed on spiders. Apparently all cantharoid members of the Tubulomandibulate Class secrete a histolytic, death-inducing fluid originating from a gland at the base of each mandible, thus allowing for rapid extraction of the fluidized prey contents (Claussen 1940, Crowson 1981). Suction of prey fluid is transferred from the mandibular food tube to the mouth proper (cibarium), unlike the situation among hydadephagans, wherein a mandibular channel carries fluid food directly to a pharyngeal region, bypassing the true mouth (Richards and Davies 1977).

Structural Themes. Tubulomandibulates consist of three major themes. Each theme is represented by a major subcluster (Fig. 72) that corresponds to a group of families or a family. These three themes are principally resolved by 13 characters that are distributed evenly among head and mouthpart regions. The characters contributing to the formation of these subclusters are gula/hypostome development, antennal type, stemmatal number, clypeal shape and segmentation, hypopharynx type, epipharynx type, mandible type, mandibular dentition, type of maxillary appendages, maxillary palp aspect-ratio and galeal modification.

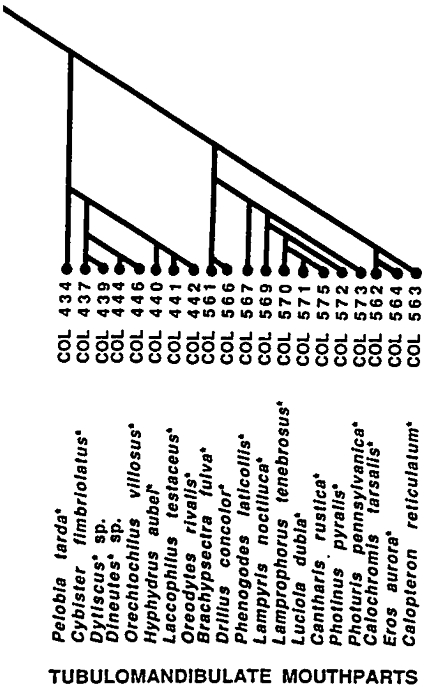

COL 434 Pelobia tarda*
COL 437 Cybister fimbriolatus*
COL 439 Dytiscus* sp.
COL 444 Dineutes* sp.
COL 446 Orechtochilus villosus*
COL 440 Hyphydrus aubei*
COL 441 Laccophilus testaceus*
COL 442 Oreodytes rivalis*
COL 561 Brachypsectra fulva*
COL 566 Drilius concolor*
COL 567 Phenogodes laticollis*
COL 569 Lampyris noctiluca*
COL 570 Lamprophorus tenebrosus*
COL 571 Luciola dubia*
COL 575 Cantharis rustica*
COL 572 Photinus pyralis*
COL 573 Photuris pennsylvanica*
COL 562 Calochromis tarsalis*
COL 564 Eros aurora*
COL 563 Calopteron reticulatum*
TUBULOMANDIBULATE MOUTHPARTS

FIGURE 72. Cluster analysis dendrogram of taxa comprising the Tubulomandibulate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart Classes.

Subcluster 1 (bracketed by data-set taxa 434 to 442 in Fig. 72) corresponds to the aquatic adephagan families Hygrobiidae (434) and Dytiscidae (all others in the subcluster). Hygrobiids and dytiscids have a dorsoventrally flattened, exserted cranial capsule with pronounced genae that fuse ventrally and dorsally and a terminally positioned labium. These forms are major predators on insects, tadpoles and small fish in freshwater ecosystems. Subcluster 2 is bracketed by taxa 561 to 573 and consists of five terrestrial families of the Cantharoidea: Brachypsectridae, Drilidae, Phenogodidae, Lampyridae and Cantharidae. Cantharoids possess a retractile, equant cephalic capsule with elongate basal sclerites of the maxillae and labium extending along most of the ventral cranial exposure. These forms prey on snails, slugs, insects and millipedes usually in litter or moss layers of forests. Subcluster 3 consists of the cantharoid family Lycidae and is differented from other cantharoids primarily by the loss or rudimentation of head- and mouthpart-related structures such as ocelli, the clypeus and the labrum.

Geochronologic History. The geochronologic history of the Tubulomandibulate Class is characterized by first a radiation of aquatic hydradephagan groups during the Early Jurassic, followed by a second radiation of several terrestrial cantharoid groups during the Early Cretaceous (Crowson 1981, Hennig 1981) (Fig. 73). Since these two superfamilial groups have been analyzed cladistically and possess a modest Mesozoic fossil record, inferences can be made regarding the approximate timing of their initial radiation.

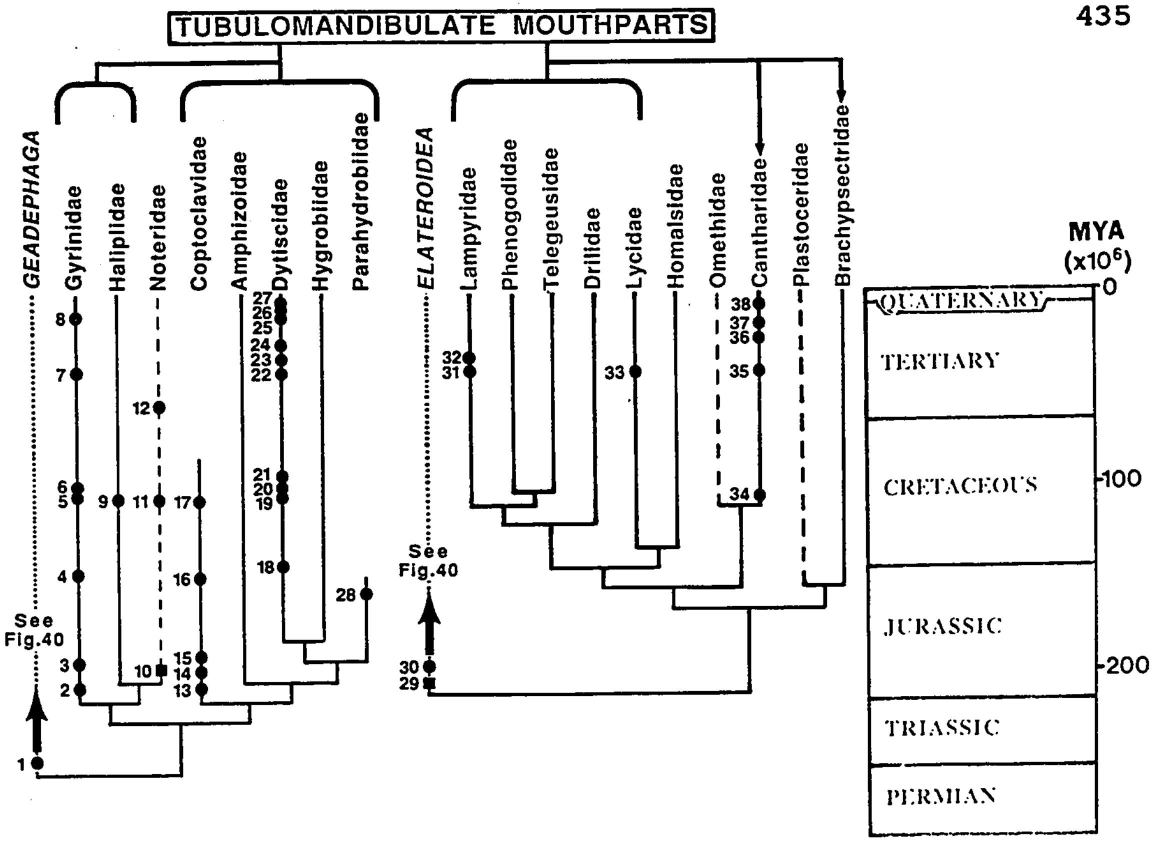


FIGURE 73. Geochronologic history of the Tubulomandibulate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Burmeister (1976), Crowson (1981) and Beutel (1986) for the Hydadephaga (but see Kavanaugh [1986] for a different view), and Crowson (1972) and Lawrence (1977a) for the Cantharoidea. The taxonomic level of analysis is the family. The outgroups are the Geadephaga and Elateroidea. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

Coleopterans of the suborder Adephaga are characterized by the unique placement of the hind coxae among coleopterans and have traditionally been divided into a terrestrial geadephagan and aquatic hydradephagan lineages. Hydradephagans are apparently monophyletic (Burmeister 1976), with the tubulomandibulate families Dytiscidae and Hygrobiidae collectively exhibiting a sister-group relationship to the Amphizoidae (Beutel 1986). Although the remaining tubulomandibulate family, the Gyrinidae, was not included in Beutel's (1986) analysis, they probably have a distant sister-group with respect to these three mandibulotubulate families within the adephagan lineage (Beutel and Rohghley 1988). Similarly, Lawrence and Newton (1982) maintained that gyrinids may be closer to the primitive adephagan stock than to the derived "dytiscoid" lineage. Others, such as Crowson (1981) and Burmeister (1976), indicate that gyrinids are a more proximal sister-group to the Amphizoidae + (Dytiscidae + Hygrobiidae) clade. The evidence suggests a monophyletic origin of tubulomandibulate mandibles within the Hydradephaga, though a diphyletic origin should be entertained.

The earliest characterizable hydradephagan is from the Lower Jurassic of the Soviet Union [67], *Angaragabus jurassicus* Ponomarenko, which is an adult member of the nontubulomandibulate family Noteridae (Ponomarenko 1963, Crowson 1981). However, the oldest demonstrable tubulomandibulate hydradephagans are adults of the gyrinid *Angarogyrus minimus* Ponomarenko and the dytiscid *Cretodytes latipes* Ponomarenko from the Upper Jurassic of the Soviet Union [60] (Ponomarenko 1973, 1977, Crowson 1981, Hennig 1981). In Jurassic deposits, larvae with falcate, robust mandibles have been assigned to the Parahydrobiidae (Ponomarenko 1977), a species that may be ancestral to modern Hydrobiidae. The earliest confidently assigned dytiscid larvae are forms bearing falcate mandibles from the Lower Cretaceous of Australia [53] (Jell and Duncan 1986). Dytiscid adults have also been described from the the early Cretaceous of Transbaikalia, Soviet Union [52] (Ponomarenko 1988b). Thus, by Late Jurassic times, aquatic members of the Tubulomandibulate Mouthpart Class existed in moderate diversity.

Within the suborder Polyphaga, which constitutes 88% of all beetles, the superfamily Cantharoidea is recognized as a distinctive group (Crowson 1981), although its monophyletic integrity has been recently doubted by Lawrence (1987). This questioning largely centers on the taxonomic affinities of *Brachypsectra*, which bridges the Cantharoidea with its sister-group, the Elateroidea. Because *Brachypsectra* possesses thin, tubulate mandibles found in several cantharoid families (Böving and Craighead 1931), it has been suggested that tubulate mandibles are autamomorphous for the Cantharoidea. However, this matter remains muddled because of the tentative systematic position of *Brachypsectra* (Crowson 1976) and the presence of several cantharoid families, some of them more plesiomorphous than cantharids or lampyrids, that lack tubulate mandibles (Lawrence and Newton 1982). Accepting a sister-group relationship between the Elateroidea and Cantharoidea and the presence of elateroid fossils from the Early Jurassic (Dolin 1973), a Late Jurassic divergence time has been proposed by Crowson (1981). Additional substantiation for this timing is the presence of a cantharid adult from the Lower Cretaceous of Victoria, Australia [53] (Jell and Duncan 1986). The Australian cantharid is the only member unequivocably found in the Mesozoic; other members occur in the Eocene/Oligocene Baltic Amber biota [19] and resemble modern genera (Larsson 1978; Ponomarenko 1988b). Clearly, by Cretaceous times, tubulomandibulate members were largely exploiting ground habitats for predaceous feeding.

Previous Designations. As far as can be determined from the available literature, the Tubulomandibulate Mouthpart Class has been associated with planipennian larval mouthparts when a distinction has been made between "generalized" mandibulate mouthparts and a specialized subset variously referred to variously as "grasping-sucking" or "mandibulo-suctorial" (Metcalf et al. 1962), "chewing- sucking" (Borror et al. 1976) or "piercing-and-sucking" (Smith 1985). When this distinction has been absent, they have been assigned a more general designation (Metcalf 1929) or not discussed (Table 6). In a review of major modifications of insect mouthparts, Chaudonneret (1984) considered dytiscid, gyrinid and lampyrid larval mouthparts as a distinct type, terming them "*pièces buccales predatrices suçeuses mandibulaires*." His characterization is the one that most closely approximates the concept of the mouthpart class that I am herein naming **tubulomandibulate**. The designation, tubulomandibulate, refers to the characteristic perforated mandibles possessed by all members of this mouthpart class.

Review of Literature. A substantial literature exists regarding tubulomandibulate mouthparts descriptions. Monographic treatments of mouthpart structure of selected genera commences with Vogel's (1915) description of the lampyrid *Lampyris noctiluca* Linneaus and Blunck's (1918) description of the dytiscid *Dytiscus marginalis* Linneaus and, more recently, Noars' (1956) work on the gyrinid *Orectochilus villosus* Müller and Honomichl's (1975) work that emphasizes the cranial musculature of the gyrinid *Gyrinus substriatus* Stephens. DeMarzo (1976a-c; 1977a,b; 1978; 1979) in a series of detailed studies particularly focusing on mandible structure, has described the mouthparts and mandible morphogenesis of genera from the major dytiscid groups, including Dytiscinae, Colymbetinae, Laccophilinae and Hydroporinae, and concludes with a discussion of the sucking apparatus. Jaboulet (1960) has presented a brief review of mouthpart structure for three haliplid genera, *Haliplus*, *Peltodytes* and *Brychius*. More cursory, shorter accounts of mouthpart structure include Burgess (1881) and Blunck (1916) for *Dytiscus marginalis* Linneaus, Balfour-Browne (1922) for the hygrobiid *Pelobius tardus* Herbst, Raj (1943) for the lampyrid *Lamprophorus tenebrosus* Walker and Gardner (1946) for the lampyrids *Luciola dubia* Oliver and *Diaphanes planus* Gorham.

8.4.4. Mouthhook Class
(Class 15)

Description. Head inconspicuous, often marginally projecting and sunken into thorax; nonproboscate; retractile. Genae and gula part of cephalopharyngeal capsule, surrounded by exogenously-derived, ensheathing tissue; lacking evidence of suture-bound cephalic sclerites. Antennae stubby or papillate, rarely absent; stemmata absent; compound eyes absent. Mouthparts mandibulosuctorial (some forms lacking a mandibular tubule?), prognathous to hypognathous, symmetrical, retractile. Food pump clypeal (?) and pharyngeal.

Clypeus quadrate to vertically elongate, fused to frons; often indistinguishable or absent. Labrum transversely elongate or quadrate; undivided; margin straight/curvilinear, lingulate, pectinate or mucronate. In others labrum not delimited externally, forming internal supportive rods. Hypopharynx withdrawn internally, forming a distinctive endoskeleton, the cephalopharyngeal apparatus. Epipharynx setate or membranous; mostly absent. Mandibles dicondylic; vertically-oriented and fused to maxillary elements; hooklike (mouthhooks), rarely falcate, with or without a tubule; edentate or rarely pectinate; musculation for adduction/abduction vertical to sagittal plane. Maxilla with stipes shaped similar to and accompanying mandible as an accessory cutting structure. Maxillary palpi abbreviated or absent; galeae and laciniae not evident. Labium with elongate "main-body" bearing rudimentary palps in some; often reduced to a lingulate lobe. Internal H-shaped hypopharynx articulating with mandibles and labial sclerites anteriorly and large, prothorax-sunken tentoropharyngeal sclerite posteriorly. Tentoropharyngeal sclerite bearing large, paired dorsal and ventral wings attached to thoracic musculature for head retraction. Interregional co-optation of mouthpart elements present.

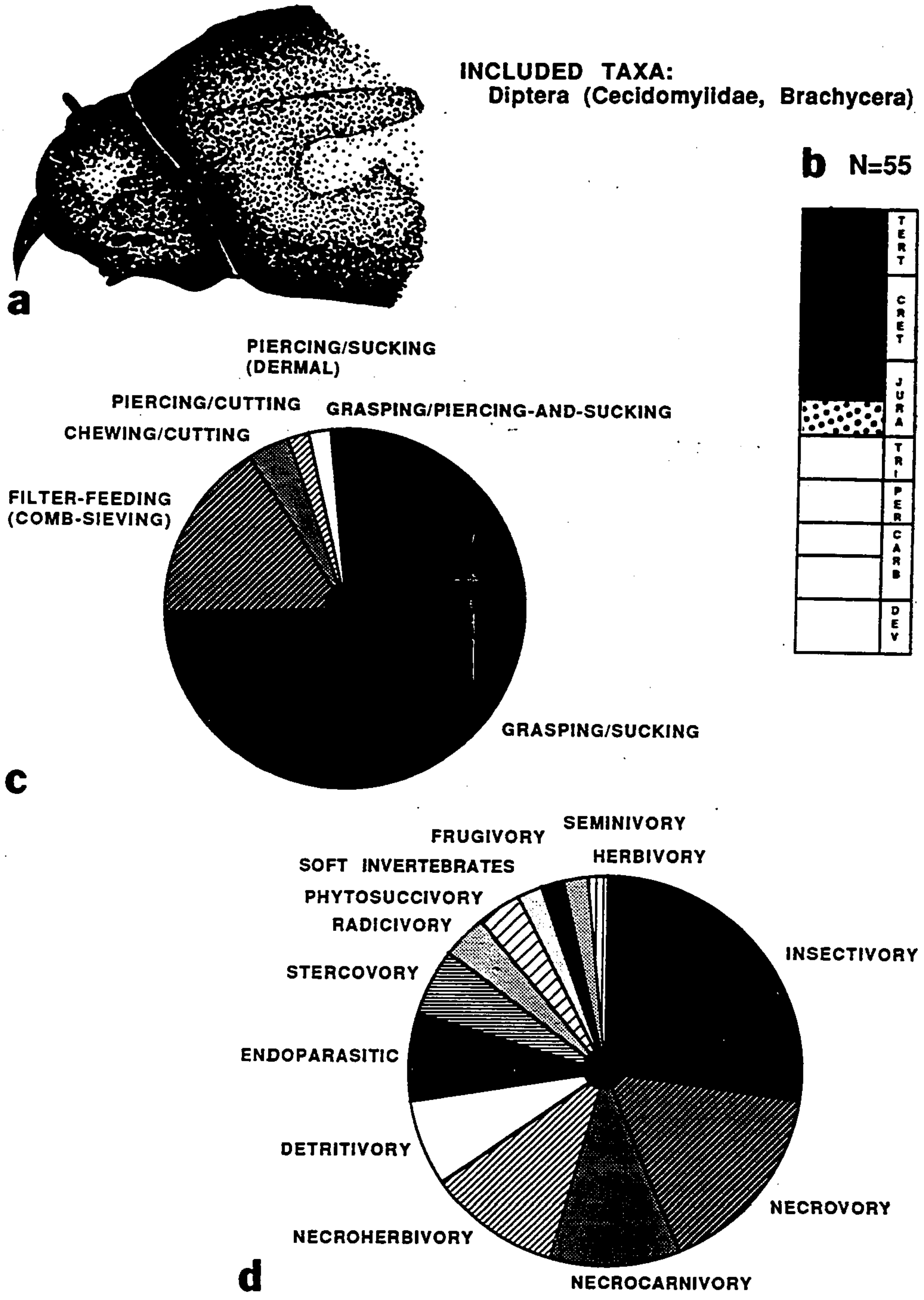
Key Phenocharacters. Mouthhook mouthparts are very distinctive because of their pronounced modification and they cannot be confused with any other mouthpart type. Characteristic features include a small, sutureless head withdrawn into the thorax, a pair of conspicuous, falcate, vertically-oriented mouthhooks, absence or extreme reduction of maxillary and labial palps, and lack of ocelli and compound eyes. The Mouthhook Class is the only mouthpart type that bears vertically-oriented mandibles.

Diversity and Natural History. The Mouthhook Class is the most diverse group within the Mandibulo-canaliculate Series, constituting about 7.6% of all hexapod species and comprising 98 families, 4,500 genera and 72,642 species of larval brachyceran dipterans (Appendix D). This species diversity translates to a rank-order six out of 34 mouthpart classes (Table 5, Fig. 131). Adult stages of the Mouthhook Class are principally labellates, although some stylate-haustellate classes are represented (Table 5). Members of the Mouthhook Class are commonly known as maggots and are usually legless, unsclerotized, vermiform larvae inhabiting the several microhabitats described below.

Typical habitats inhabited by members of the mouthhook class include carrion, dung, rotting wood, large fungal sporocarps, fermenting fruit, the internal tissues of animals (endoparasitoids) and leaves (leaf-miners). Features of virtually all of these habitats include their ephemeral nature, patchy spatial distribution, varied internal structure and presence of a unique, high-quality food resource. Because of the restricted spatiotemporal setting of these habitats, immediate colonization of such a sizable food resource is essential to potential consumers who will be competing with other taxa of the same functional-feeding-group (Kukor and Martin 1987, Braack 1987). In fact, carrion communities in vertebrate carcasses are one of the few habitats where intraspecific and interspecific competition has been demonstrated to structure internal community dynamics (Jermy 1985, Braack 1987, Peschke et al. 1987). The intensity of consumption of temporally and locally restricted but abundant food resources is partially offset by partitioning of the food resource into numerous substrates. Each substrate is consumed by a functional-feeding-group (often dominated by members of the Mouthhook Class) specializing on a particular tissue type at a particular stage of decay.

Regardless of their habitat, food consumed by members of the Mouthhook Class (Fig. 74) is characterized by several qualities. First, it involves usually dead tissue (parasitoidism and leaf-mining excepted) that is at some stage of decay. Mouthhook Class members are mostly necrovores and range from necrocarnivory (carrion) to necroherbivory (fermenting fruit) to necrolignivory (rotting logs) to stercovory (cow pies) to necrofungivory (decomposing basidiomycete sporocarps). Secondly, as the formerly solid-food resource decomposes, it is transformed into a solid-fluid mixture, then to a fluid consistency as decomposition progresses and eventually back to a solid state as the food dessicates (Smith 1986a). Thirdly, although limited in space and time, food resources by insects with mouthhook mouthparts are of exceptionally high dietary quality when compared of phytophagy in other mouthpart classes, and is nutritionally supplemented by primary decomposing micro-organisms such as bacteria, yeasts and various protozoans.

Carrion is perhaps the best-studied of these habitats and food resources, principally because of the contribution that forensic



INCLUDED TAXA:
Diptera (Cecidomyiidae, Brachycera)

FIGURE 74. Overview of the Mouthhook Mouthpart Class. a, *Canace macateei** Malloch (Diptera: Canaceidae, data-set no. 984); b, taxonomic composition, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

entomology has made to solving crimes involving human corpses. Studies on exposed, buried and submerged cadavers has revealed an intricate partitioning of food resources based on tissue type and state of decay (Smith 1986a, Peschke et al. 1987). Various studies have identified from five to eight discrete stages of human and nonhuman corpse decomposition, in which members of the Mouthhook Class are prominent in the first half of the decay process and adult mandibulates (mostly beetles) during the last half of the decay process (Smith 1986a, Braack 1987, Peshke et al. 1987). Members of the Mouthhook Class that dominate the earliest stages of decomposition are maggots of the Calliphoridae and Sarcophagidae (Frost 1959, Braack 1987).

Decomposing wood exhibits a somewhat different fauna (Hamilton 1978), although it is also rich in members of mouthhook-bearing fly larvae, some of which consume rotting wood and its microbial inhabitants. Most mouthhook inhabitants of rotting wood are predatory on wood consuming larvae (Frost 1959, Teskey 1976). Fleshy fungal sporocarps, like carrion, are additionally an ephemeral resource, persisting from a few days to a few weeks (Ashe 1984b, Kukor and Martin 1987). In these microhabitats, especially fleshy gilled mushrooms, fly larvae dominate the fauna (Bruns 1984), although it is supected that few of these inhabitants are obligate mycetobionts and are predators on fungus-consuming larval and adult insects (Kukor and Martin 1987). Vertebrate dung is another habitat and food resource used by several families of fly larvae, including scatopsids, helomyzids, anthomyiids, sarcophagids, sapromyzids, muscids and others (Frost 1959). Many fly larvae are also parasitoids of other larval or adult insects and use their mouthhooks and associated mouthpart structures as anchors and feeding organs on particular internal tissue substrates. Prominent parasitoids include tachinids and, to a lesser extent, other calyptrate muscomorphan families (Clausen 1940). Finally, it is notable that leaf-mining as a habitat-type and feeding behavior has been entered not only by sericterates (see Section 8.3.14) but also by members of the Mouthhook Class, particularly agromyzids, tephritids and chloropids (Hering 1951, Lawton 1976, Brown and McGavin 1982, Aderkas and Peterson 1987).

Structural Themes. Three major themes are indicated by the subclustering patterns of mouthhook mouthparts in Fig. 75. These themes encompass approximately 75% of dipteran superfamilial diversity and include advanced nematocerans, brachycerans and cyclorrhaphans. Approzimately 16 characters account for the separation of mouthhook mouthparts into subclusters and most of these involve mouthpart reduction series or modifications of the mouthhooks. The 16 characters responsible for most of the separation of taxa into subclusters, with two exceptions, originate from four mouthpart fields--general features of mouthpart apparati, and the pharyngeal, mandibular and maxillary regions.

Subcluster 1 (bracketed by data-set nos. 859 to 883 in Fig. 75) consists of cecidomyiid nematocerans and tabanoid, asiloid and empidoid brachycerans; 24 taxa from 12 families are represented. Taxa of this subcluster have the highest complement of head and mouthpart elements of the three subclusters and they often possess pronounced falcate or cupulate mandibles. Subcluster 2 (data-set nos. 895 to 1027) consists

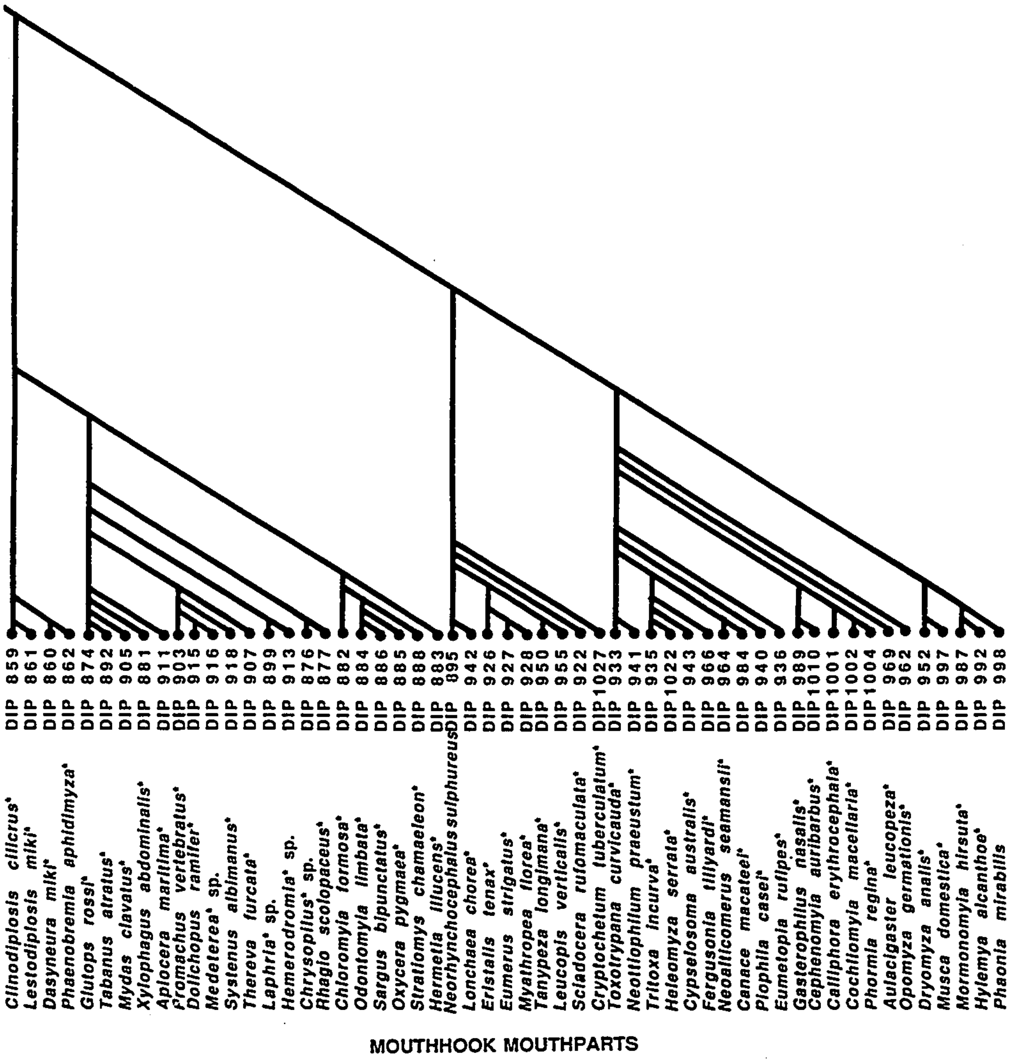
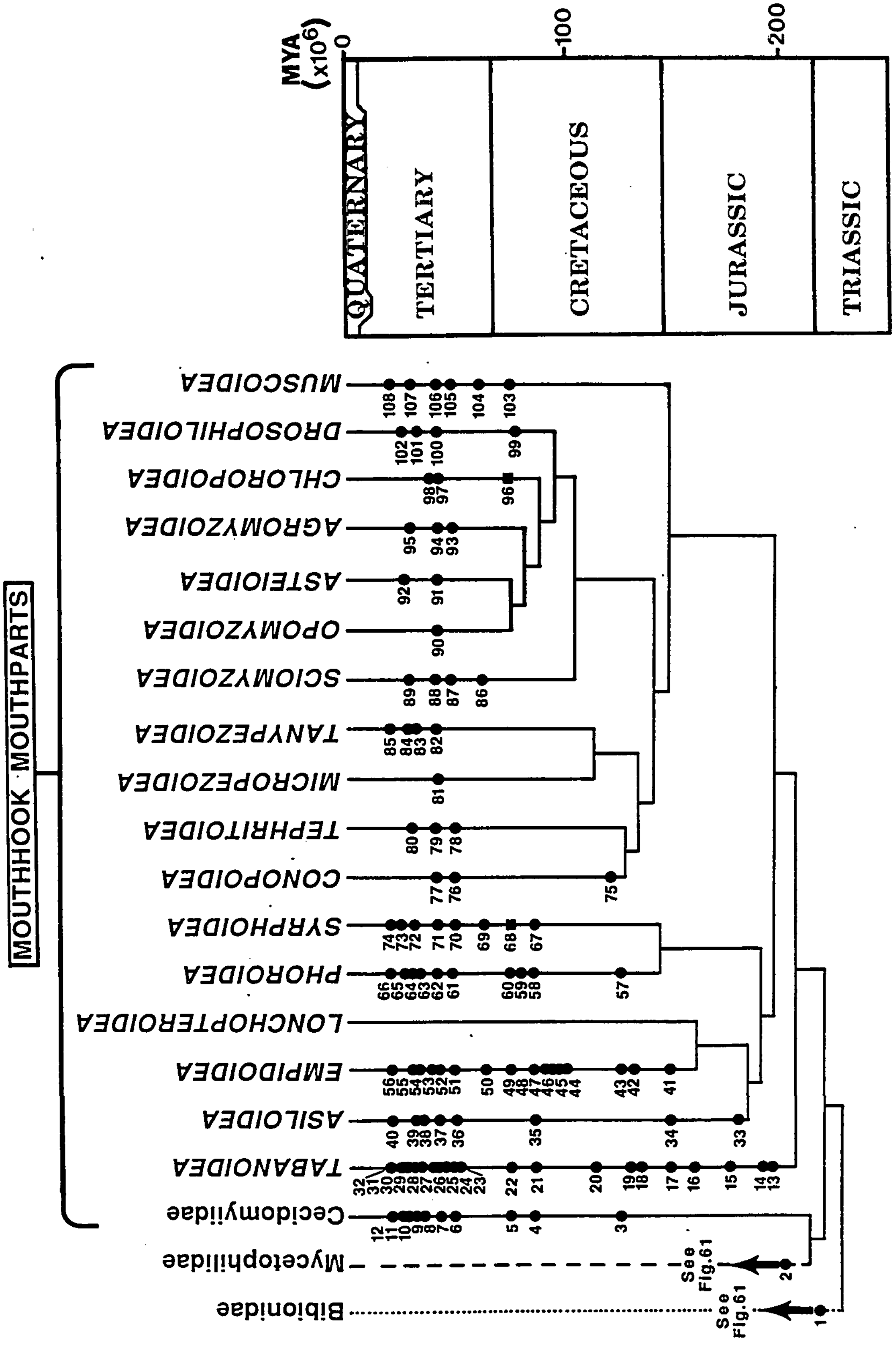

Clinodiplosis cilicrus* DIP 859
Lestodiplosis mikii* DIP 861
Dasyneura mikii* DIP 860
Phaenobremia aphidimyza* DIP 862
Glutops rossi* DIP 874
Tabanus atratus* DIP 892
Mydas clavatus* DIP 905
Xylophagus abdominalis* DIP 881
Apiocera maritima* DIP 911
Promachus vertebratus* DIP 903
Dolichopus ramifer* DIP 915
Medetera* sp. DIP 916
Systenus albimanus* DIP 918
Thereva furcata* DIP 907
Laphria* sp. DIP 899
Hemerodromia* sp. DIP 913
Chrysopilus* sp. DIP 876
Rhagio scolopaceus* DIP 877
Chloromyia formosa* DIP 882
Odontomyia limbata* DIP 884
Sargus bipunctatus* DIP 886
Oxycera pygmaea* DIP 885
Stratiomys chamaeleon* DIP 888
Hermetia illucens* DIP 883
Neorhynchocephalus sulphureus DIP 895
Lonchaea chorea* DIP 942
Eristalis tenax* DIP 926
Eumerus strigatus* DIP 927
Myathropa florea* DIP 928
Tanypeza longimana* DIP 950
Leucopis verticalis* DIP 955
Sciadocera rufomaculata* DIP 922
Cryptochetum tuberculatum* DIP1027
Toxotrypana curvicauda* DIP 933
Neottiophilum praeustum* DIP 941
Tritoxa incurva* DIP 935
Heleomyza serrata* DIP1022
Cypselosoma australis* DIP 943
Fergusonia tillyardi* DIP 966
Neoalticomerus seamansi* DIP 964
Canace macateei* DIP 984
Piophila casei* DIP 940
Eumetopia rufipes* DIP 936
Gasterophilus nasalis* DIP 989
Cephenomyia auribarbus* DIP1010
Calliphora erythrocephala* DIP1001
Cochliomyia macellaria* DIP1002
Phormia regina* DIP1004
Aulacigaster leucopeza* DIP 969
Opomyza germationis* DIP 962
Dryomyza anilis* DIP 952
Musca domestica* DIP 997
Mormonomyia hirsuta* DIP 987
Hylemya alcanthoe* DIP 992
Phaonia mirabilis DIP 998
MOUTHHOOK MOUTHPARTS

FIGURE 75. Cluster analysis dendrogram of taxa comprising the Mouthhook Mouthpart class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

of a nemestriniid brachyceran and aschizan and primitive schizophoran cyclorrhaphans; nine taxa from seven families are represented. These taxa exhibit the greatest reduction of mouthpart elements and are characterized by missing clypeus, labra (sometimes only reduced), galeae and laciniae. Members bear mouthhooks that are short and hooklike, or less often cupulate. Subcluster 3 consists of primitive and derived schizophoran cyclorrhaphans; 22 taxa from 17 families and nine superfamilies are present. This subcluster exhibits modest mouthpart reduction, with the galeae and laciniae absent but the clypeus and labrum present; the mouthhooks are tubulate and falcate. These three themes are characterized overall by a reduction series of mouthpart elements and by structural modifications of the mouthhooks.

Geochronologic History. Since the mouthhook mouthpart class approximately corresponds to larval brachycerous dipterans (nematocerans lack mouthhooks), the timing of the earliest occurrence of the mouthhook mouthpart class centers on the presumed time of divergence between the Brachycera and its sister-group, the Bibionomorpha (Hennig 1981). Based on the presence of diverse bibionomorph taxa described from the Upper Triassic of central Asia [73], including forms such as *Rhaetomyia*, *Protobliogaster* and *Protorhyphus* that are unassignable to modern families but apparently are referable to the Bibionomorpha (Rohdendorf 1974, Hennig 1981, but see Carpenter and Burnham 1985), the earliest indirect evidence for mouthhook mouthparts is Late Triassic (Fig. 76). All Late Triassic dipteran fossils are adults, particularly wings, disallowing direct confirmation of the presence of mouthhook mouthparts.

FIGURE 76. Geochronologic history of the Mouthhook Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Rohdendorf (1980) and McAlpine and Wood (1989). The level of taxonomic analysis is the superfamily. The outgroup is Bibionidae. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.


MYA ($\times 10^6$)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
MOUTHHOOK MOUTHPARTS
MUSCOIDEA
DROSOPHILOIDEA
CHLOROPOIDEA
AGROMYZOIDEA
ASTEIOIDEA
OPOMYZOIDEA
SCIOMYZOIDEA
TANYPEZOIDEA
MICROPEZOIDEA
TEPHRITOIDEA
CONOPOIDEA
SYRPHOIDEA
PHOROIDEA
LONCHOPTEROIDEA
EMPIDOIDEA
ASILOIDEA
TABANOIDEA
Cecidomyiidae
Mycetophilidae
Bibionidae
See Fig.61
See Fig.61

The earliest brachyceran fossil is an asilomorph wing from the Lower Jurassic of East Germany [68] described by Handlirsch (1937) and affirmed by other studies (Hennig 1967; Rohdendorf 1974; Kovalev 1981, 1985). Somewhat younger deposits from the Early/Middle Jurrasic boundary of the Irkutsk Region, Soviet Union [67] have yielded several genera assignable to two tabanoid lineages, the Rhagionidae and an unspecified second group (Kovalev 1981, 1982, 1985). By the end of the Jurassic, the superfamilies Bombyloidea (Nemestrinidae, Acroceridae) and Empidoidea (*Protempis*) were added (Rohdendorf 1980, Kovalev 1985, Kalugina and Kovalev 1985), indicating a significant diversity of eight families of predaceous and anthiphilous asilomorphs. This trend constitutes additional direct evidence for the occurrence of mouthhook mouthparts during the Jurassic.

During the earliest Cretaceous, the first direct evidence for mouthhook mouthparts is provided by the earliest brachyceran larva. In Lower Cretaceous deposits of Spain [56], at least four unnamed brachyceran larvae are known, two which are stratiomyids, a sciomyzid and a specimen of uncertain familial affinity (Condal 1951, Teixeira 1954, Whalley and Jarzembowski 1985). Some of these specimens contain mouthhooks and, occasionally, details of the cephalopharyngeal apparatus. In slightly younger Lower Cretaceous strata of Australia [53], an indistinct brachyceran larva has been reported (Jell and Duncan 1986). Additionally, this deposit, together with material from the earliest Cretaceous Lebanese amber [55], has yielded the earliest fossils of cyclorrhaphan dipterans (Hennig 1971, Jell and Duncan 1986), consisting of complete adult specimens unassignable to recent families. Younger, Upper Cretaceous amber deposits from northwest France [45] (Schlüter 1975, 1978), the Taimyr Peninsula of the USSR [37] (Zherikin and Sukachaeva 1973, Negrobov 1978, Kovalev 1985) and Cedar Lake in Canada [35] (McAlpine and Martin 1966, 1969; McAlpine 1970, 1973) have provided ample evidence for a diversification of cyclorrhaphan taxa, most of which were associated with anthophilous habits probably associated with the emergence of flowering plants (Willemstein 1987). This radiation of cyclorrhaphan dipterans is essentially complete by Baltic amber times [19], as evidenced by the occurrence in Baltic amber of most of the derived modern acalyptrate schizophorans and nonparasitic calyptrates (Hennig 1965, Larsson 1978).

Previous Designations. Mouthhook mouthparts have commonly been referred to as "reduced" or "degenerate" (e.g. Metcalf et al. 1962; Chaudonneret 1983), or they have been recognized as a discrete mouthpart type with a unique, although highly modified, function (James and Harwood 1969). Most synthetic studies of mouthparts do not make reference to mouthhook mouthparts at all (see Table 6). In this study, the characterization of mouthhook mouthparts as "degenerate" is rejected. Although the heads and mouthparts of brachyceran larvae are highly reduced structurally as a consequence of a saprophagic existence, they nevertheless possess a few prominent, structurally unique mouthpart elements--mandibular and occasionally maxillary mouthhooks--that are an efficient mechanism for obtaining fluid food. This condition is contrasted with the truely reduced mouthparts of the Nontrophic Class

(Sect. 8.10.3), wherein extreme reduction of mouthparts as well as inability to procure or process food permits a degenerate designation to be truely meaningful.

I have appropriated the term **mouthhook** to refer to the conspicuous structures characterizing the distinctive external nature of larval brachyceran mouthparts. The term is well-established in literature on the Diptera and is an appropriate designation for this mouthpart class.

Review of Literature. Much of the literature on mouthhook mouthparts consists of short descriptions of new species or studies of the life history and feeding ecology of selected species. Few monographic accounts exist. The few notable exceptions are Ludwig's (1949) study of *Calliphora erythrocephala* (Meigen), Schremmer's (1962) work on *Stratiomys chamaeleon* Linneaus and several other brachyceran larvae, and Vaillant and Delhom's (1956) examination of the stratiomyiids *Odontomyia limbata* Meigen, *Oxycera torrentium* Vaillant and *Chloromyia formosa* Scopoli. Recent accounts of mouthpart morphology and ecology of dipteran larvae inhabiting special habitats include Teskey's (1976) description of larvae frequenting decaying North American trees and Smith's (1986b) description of larvae occurring in carrion of northern Europe and Great Britain. Compendia of mouthpart structures are Peterson's (1951) somewhat dated catalog of North American dipteran larvae and the excellent, three-volumed *Manual of Nearctic Diptra* edited by McAlpine, et al. (1981, 1987).

Numerous shorter accounts of head and mouthpart structure of brachyceran larvae is the source for most of my data. For orthorrhaphans, Teskey (1970) described the pelecorhynchid *Glutops rossi* Pechuman; Greene (1926) presented accounts of several species of tabanoids, particularly stratiomyiids; Crouzel and Salavin (1943) studied the nemestrinid *Neorhynchocephalus sulphureus* (Wiedemann); Fuller (1938) examined the bombyliid *Cyrtomorpha flaviscutellaris* Roberts; and Wirth (1952) gave a description of the dolichopodid *Systenus apicalis* Wirth. As for the head capsule and mouthpart morphology of aschizan cyclorrhaphans, a description of the sciadocerid *Sciadocera rufomaculata* White was provided by Fuller (1934). Acalyptrate schizophoran cyclorrhaphans were the most diverse group of brachycerans described and included Greene's (1929) description of several tephritid larvae; Valley, Novak and Foote's (1969) account of the otitid *Eumetopiella rufipes* (Macquart) and Allen and Foote's (1967) description of four otitid species; Tate's (1954) study of the piophilid *Neottiophilum praestum* (Meigen); McAlpine's (1966) description of the cypselosomatid, *Cypselosoma australis* McAlpine; Foote's (1970) examination of the tanypezid *Tanypeza longimana* Fallén; Sluss and Foote's (1971) similar examination of the chamaemyiid *Leucopis verticalis* Malloch; a series of articles by Thomas (1933, 1934, 1938) on three grain-infesting opomyzids; Shewell's (1960) description of the odiniid *Neoalticomerus seamansi* Shewell; Lobanov's (1970) description of the heleomyzid *Heleomyza serrata* Linneaus; and Hennig's (1935) initial description of the michilid *Leptometopa* sp. Finally, studies of calyptrate schizophoran cyclorrhaphans, synonymous with the Superfamily Muscoidea, include Roberts' (1971) functional-morphological account of the calliphorid *Calliphora vomitoria* (Linneaus) and the predaceous muscid *Limnophora riparia* Fallén; and Cameron's (1932) account of the oestrid *Cephenomyia auribus* Meigen, commonly known as the nasal botfly.

8.5. Labellate Series

8.5.1. General Features of the Labellate Series

General Structure. The Labellate Series comprises a taxonomically diverse assemblage characterized by a protruding, fleshy, sponging or rasping organ used for food acquisition. Associated with this organ is a dorsoventrally-prolonged head that bears hypognathous mouthparts. Sense organs are conspicuous and well-developed: eyes are large and hemispherical and ocelli are three in number, rarely wanting. Mandibles are absent or vestigial. The labrum and epipharyngeal surface forms a dorsal roof over the sponging organ, forming a food canal for transporting food cephalad to the mouth.

Although the sponging or rasping organ for various taxonomic groups is termed a hypopharynx, "haustellum," labellum, proboscis, or haustorium (the latter proposed herein for trichopterans), it is the key feature of the Labellate Series. This fleshy, hypognathous organ is derived from the hypopharynx, the palpal region of the labium, or elements from both, to form a composite structure. The food contacting surface of this organ bears pseudotracheae that, by capillary flow, passively absorbs surface fluid and fluid-suspended particles and is supplemented by a pharyngeal or clypeal (cibarial) pump at the organ base for active transport of food orally. In some forms, modification of pseudotracheal denticles into short, aciculate structures for rasping skin or cuticle has supplanted surface sponging of fluids.

Included Classes. The Labellate Series comprises the Haustoriate and Labellate Mouthpart Classes. (See Table 5 for taxonomic membership, life-stages and number of taxa examined for each mouthpart class.)

Diversity and Other Distributional Patterns. The Labellate Mouthpart Series constitutes adult holometabolous forms that fluid-feed by sponging and rasping surface tissue. Although orthopteran gryllids (crickets) bear a fleshy hypopharynx convergent with the haustorium of trichopterans (Rietschel 1953), they are excluded from the Labellate Series, and are a subcluster of the adult-ectognathate mouthpart class (Section 8.3.4, Fig. 36d). This series has achieved a moderate diversity when compared to other mouthpart classes. Although members of the Siphonate and Glossate Series are also surface fluid-feeders, the Labellate Series includes a more catholic variety of diets. Their dietary repertoir includes surface exudates of all kinds--honeydew (Downes and Dahlem 1987), deliquescing fungal sporocarps (Kukor and Martin 1987), perspiration (Huckett and Vockeroth 1987), fruit sap (Wheeler 1987), fluidized carrion (Smith 1986a, Braack 1987), dung (Kevan and Baker 1983) and blood (O'Meara 1987), as well as the nectar and pollen that typifies the diets of siphonates and glossates. Members of the Labellate Class, consisting of nannochoristan mecopterans and brachycerous dipterans, are important pollinators in temperate and tropical ecosystems (Armstrong 1979, Yumoto 1987, Stork 1987). All three classes, however, partake of nutritive fluid foods occurring either at the surface or subdermally in substrates that are accessible by a sponging or rasping organ.

As members of the Labellate Class, brachycerous dipterans, constitute a very diverse suite of anthophilous pollinators. Labellates are dominanant participants in a characteristic type of pollination that consists of two major themes (Faegri and van der Pijl 1980). First is the "small fly blossom syndrome," comprising flowers with shallow, radially-symmetrical, small corollas with exposed sexual organs (Crepet 1979, Kevan and Baker 1984). Secondly, the "sapromyophilous syndrome" is characterized by deep, radially-symmetrical flowers, often with deeply hidden sexual organs. Sapromyophilous flowers often are the color of decaying flesh and release volatile scents mimicing the odor of carrion (Kevan and Baker 1984). Haustoriates do not appear to be particularly involved in these pollination syndromes, although they probably are unrecognized nectar-feeders (Porsch 1958).

Major Structural Variations. Two major directions characterize mouthpart development within the Labellate Series. One is simple expansion of a hypopharynx into a large, fleshy organ for sponging, replete with dermal pseudotracheae for the increased surface area necessary for capillary flow. This tack also has been taken by adult trichopterans. A second approach, taken by nannochoristan mecopterans and brachycerous dipterans, is conversion of two-segmented labial palpi into an prominent fleshy, sponging organ. This has been done by expanding the dermal surface area of the palp terminus, shortening palpal length, and mesial fusion of the palps. Additionally, dipterans possess a lever-based protraction/retraction system for movement of the proboscis cephalad when not in use.

Geochronologic Range. The Haustoriate Class may be represented in Lower Permian sediments of Kansas [90], based on the earliest appearance of the Order Trichoptera (Carpenter and Burnham 1985). This assumes that the extinct suborder Permotrichoptera (Sukacheva 1976) possessed wing-related synapomorphies with the Diptera and not the Trichoptera (Hennig 1981) and lacked a haustoriate hypopharynx. Wong (1983) has assigned Middle Jurassic specimens from China [64] to the extant trichopteran suborder, Annulipalpia. These Jurassic fossils provide clear evidence for the existence of the Labellate Series minimally by Middle Jurassic time. Finally, in an Lower Cretaceous, preangiospermous insect fauna from Australia [53], Jell and Duncan (1986) have referred a larval case and pupae to two recent trichopteran families. This strongly indicates presence of the Labellate Series before the advent of angiosperms as dominant floral elements. Members of the Labellate Class can be traced to the Lower Jurassic (Rohdendorf 1974, Krzeminski and Kovalev 1988), based on tipulid wing fossils and by indirect association with extant confamilial members that bear fleshy labellae.

8.5.2. Haustoriate Class
(Class 16)

Description. Head squarose to sometimes dorsoventrally prolonged; proboscate; nonretractile. Cephalic capsule with distinct or indistinct frons, sometimes fused to clypeus. Genae prominent; gula moderately developed to absent. Antennae setaceous or filiform; ocelli 3 or absent; compound eyes prominent, dichoptic. Mouthparts labellate; hypognathous; symmetrical; retractile. Food pump clypeal and pharyngeal.

Clypeus quadrate and fused to frons. Labrum vertically elongate to quadrate; undivided; margin straight/curvilinear or acute. Hypopharynx a conspicuous, labellate structure, often multilobate, bearing a network of numerous, impressed pseudotracheae and salivary orfice on distal surface; epipharynx sulcate, bordered by setae. Mandibles quadrangular or vestigial lobes; musculation not evident. Maxillary main-body of 2 sclerites; stipes equant; bearing galeae and palpi, rarely a lacinia. Maxillary palpus filiform; 4- or 5-segmented, rarely 1- or 3-segmented; long. Galea lingulate; lacinia generally absent, or a pectinate comb. Labium with elongate main-body of 2 or 3 sclerites; generally bearing labial palps, infrequently a ligula. Labial palps filiform; 3-segmented; long. Glossae mucronate or absent; paraglossae absent, or lingulate if present.

Key Phenocharacters. The most unique feature of haustoriate mouthparts is presence of a pronounced, retractile, pseudotracheate hypopharynx that is functionally analogous but anatomically different from the labellum of labellate mouthparts (Sect. 8.6.2). The haustorium in trichopterans is quite similar in placement, gross surface structure and overall shape to the dipteran labellum. Although the haustoriate head shares hypognathous mouthparts with labellates, it is different in suture location, ocellar placement, frons shape and antennal structure.

Diversity and Natural History. The haustoriate mouthpart class consists of trichopterans (caddisflies). Trichopterans sponge their food by capillary action of pseudotracheae on prominent, fleshy hypopharynges (Crichton 1957), and imbibe fluid food directly. Although widespread consumption of food by adult trichopterans is a debatable issue, as discussed below, they are a moderately diverse clade in the modern fauna. Haustoriates constitute 39 families, 650 genera and about 6,500 species (Appendix D), which translates to a rank-order of 18 out of 34 mouthpart classes (Table 5, Fig. 131). Compared to other mouthpart classes, haustoriates are an ecologically minor group.

Adult trichopterans are winged but poor flyers, live only a few weeks and are associated with plants above ground level. Although the adults are commonly considered nonfeeders (Richards and Davies 1977, Milne and Milne 1980), anecdotal evidence indicates that many are active fluid feeders, imbibing nectar and water (Fig. 77). Adult trichopterans are implicated as minor pollinators of plants because of their affinity for nectar (Proctor and Yeo 1973) and have been observed to feed on European plants as diverse as *Hedera* (ivy), *Valeriana* (valerian), *Nuphar* (yellow waterlily), *Spiraea* (spiraea), *Gentiana* (gentian), *Ranunculus* (buttercup) and *Listera* (twayblade) (Döhler 1915, Crichton 1957, Porsch 1958). Also, adult trichopterans readily take up sugar solutions in laboratory observations (Crichton 1957), indicating an ability to feed on floral or extrafloral nectaries. These observations, in conjunction with the relatively elongate, highly developed proboscides of some forms

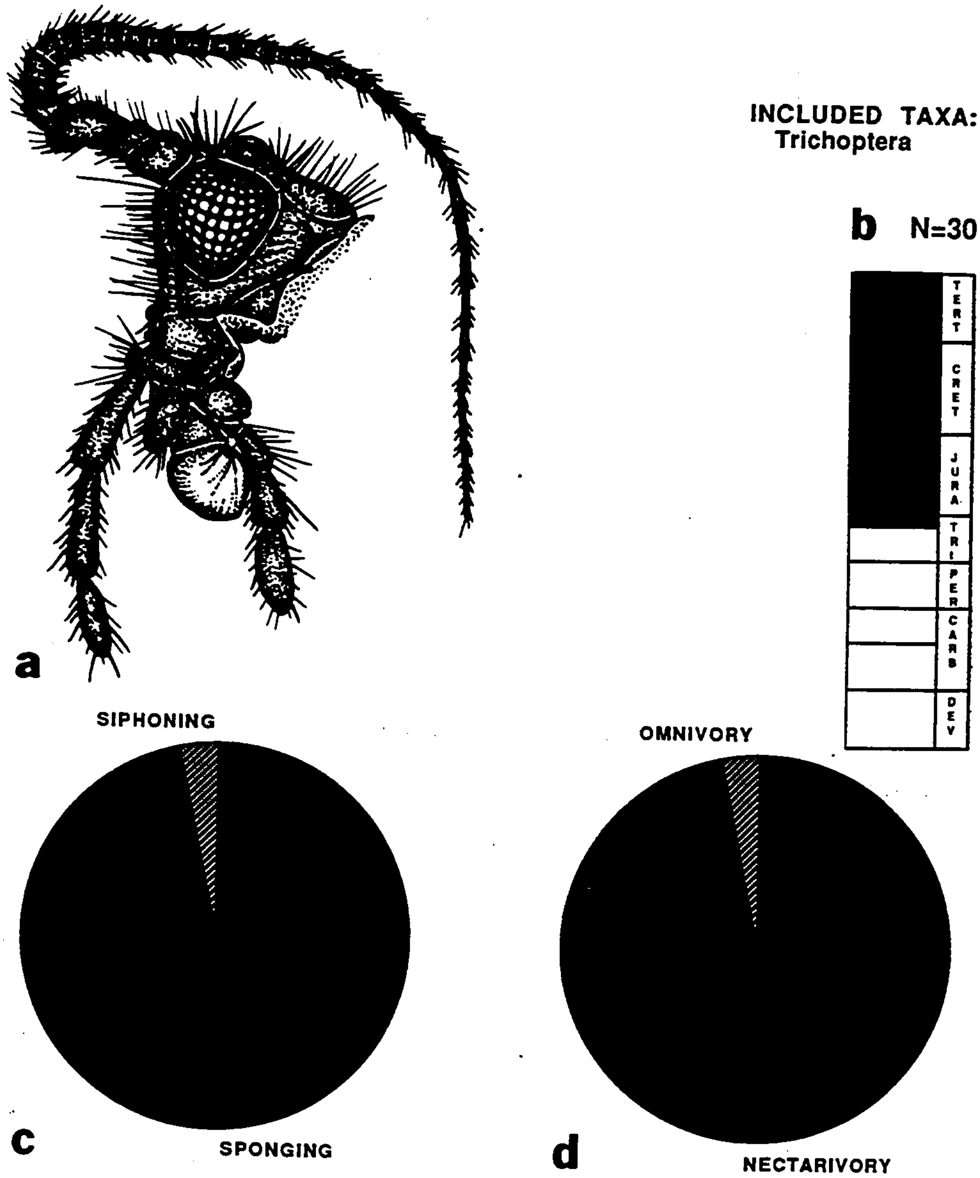


FIGURE 77. Overview of the Haustoriate Mouthpart Class. a, *Phryganea striata* Linneaus (Trichoptera: Phryganeidae, data-set no. 1050), after Crichton (1957); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

(Cummings 1914a), indicates that trichopterans represent significant but not dominant agents of pollination in some ecosystems.

Structural Themes. Haustoriate mouthparts are characterized by five major patterns of subclustering, or themes (Fig. 78). The general pattern of haustoriate subclustering consists of: (i) a large subcluster of 21 taxa representing 17 families from all three superfamilies of trichopterans, (ii) a smaller, secondary subcluster of a rhyacophiloid and five limnephiloid families and (iii) three monotaxic subclusters of structurally aberrant forms. Sixteen characters from seven of the nine head- and mouthpart regions (Appendix A) have character-state distributions on haustoriate taxa that resulted in the subclustering patterns. General head and labial characters are richly represented.

Subcluster 1 (bracketed by data-set nos. 1029 to 1073 in Fig. 78) constitutes the foundation of haustoriate mouthparts since it contains members from all of the three superfamilies and almost half of the families of the order. The unity of this subcluster is evident from the high degree of chaining and relative paucity of hierarchical branching. Taxa of Subcluster 1 are typical trichopterans with a fleshy, often pseudotracheate haustorium. Subcluster 2 (data-set nos. 1032 to 1083) is a motley assemblage of dominately Oceanian forms with several differences in mouthpart structure, especially maxillary elements, that are sufficiently pronounced for exclusion from Subcluster 1. The three remaining monotaxic subclusters are the plectrotarsid *Plectrotarsus gravenhorstii* (Subcluster 3, 1068), the dipseudopsid *Dipseudopsis africana* (Subcluster 4, 1045) and the stenopsychid *Pseudostenopsyche*

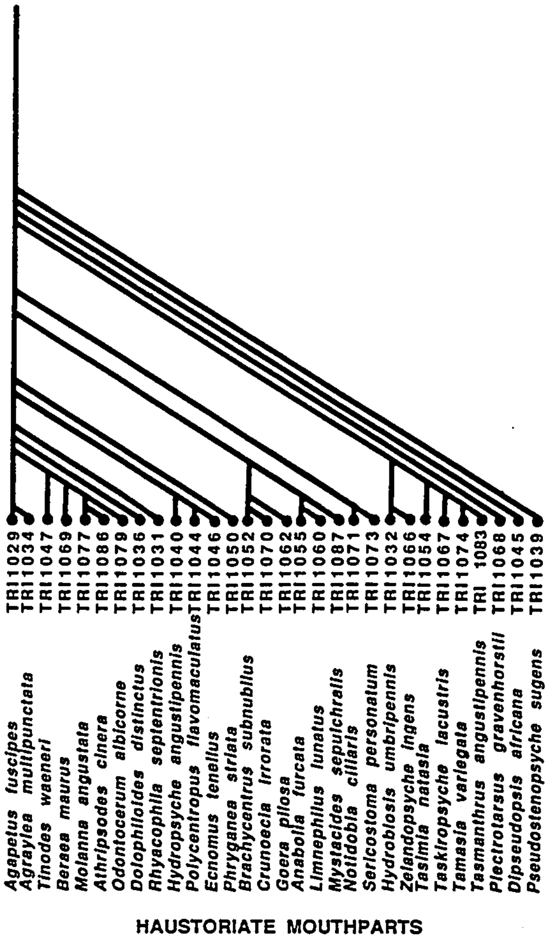
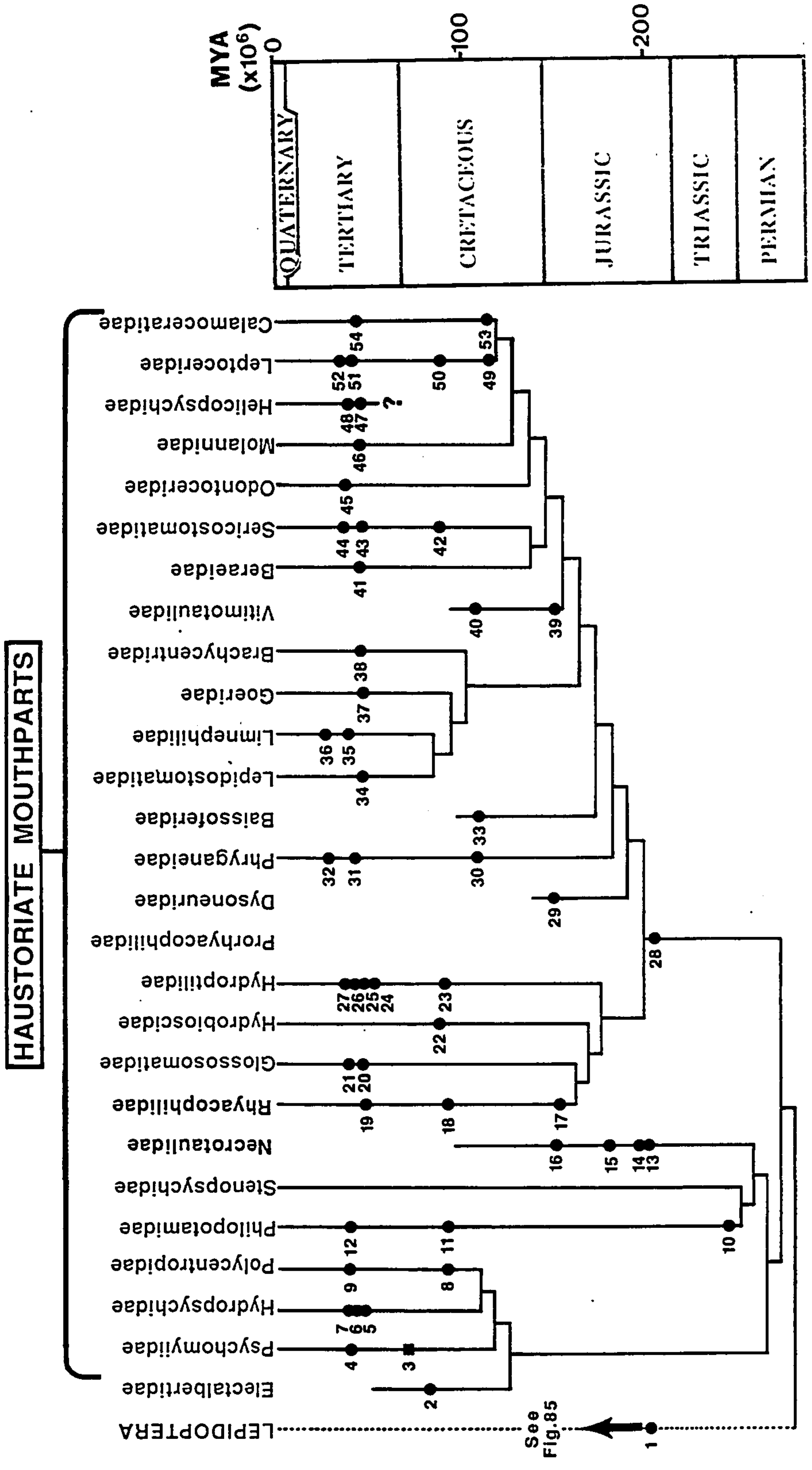

Agapetus fuscipes TRI1029
Agraylea multipunctata TRI1034
Tinodes waeneri TRI1047
Beraea maurus TRI1069
Molanna angustata TRI1077
Athripsodes cinera TRI1086
Odontocerum albicorne TRI1079
Dolophiloides distinctus TRI1036
Rhyacophila septentrionis TRI1031
Hydropsyche angustipennis TRI1040
Polycentropus flavomaculatus TRI1044
Ecnomus tenellus TRI1046
Phryganea striata TRI1050
Brachycentrus subnubilus TRI1052
Crunoecia irrorata TRI1070
Goera pilosa TRI1062
Anabolia furcata TRI1055
Limnephilus lunatus TRI1060
Mystacides sepulchralis TRI1087
Notidobia ciliaris TRI1071
Sericostoma personatum TRI1073
Hydrobiosis umbripennis TRI1032
Zelandopsyche ingens TRI1066
Tasimia natasia TRI1054
Taskiropsyche lacustris TRI1067
Tamasia variegata TRI1074
Tasmanthrus angustipennis TRI 1083
Plectrotarsus gravenhorstii TRI1068
Dipseudopsis africana TRI1045
Pseudostenopsyche sugens TRI1039
HAUSTORIATE MOUTHPARTS

FIGURE 78. Cluster analysis dendrogram of taxa comprising the Haustoriate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

sugens (Subcluster 5, 1039). These three taxa exhibit pronounced peculiarities of certain mouthpart elements, particularly the elongate ventral expansion of the haustellum and prolongation of the galeae into a lepidopteran-type proboscis (see Crichton, 1957).

Geochronologic History. Trichopteran wing venation lacks synapomorphies that distinguish it from its sister-group, Lepidoptera (Hennig 1981, Kristensen 1984b) and thus the geochronologic history of haustoriate mouthparts is difficult to ascertain. While all modern trichopterans possess a large, fleshy, pseudotracheate hypopharynx, it is not clear whether the immediate ancestors of the trichopterans, the stem-group Amphiesmenoptera (=Trichoptera + Lepidoptera), bore the haustoriate mouthparts of trichopterans, the mandibulate mouthparts of zeuglopteran lepidopterans, or the probable rostrate mouthparts of ancestral mecopterans. Cladistic analyses of the five related mecopteroid orders indicates that the Mecoptera + (Diptera + Siphonaptera) forms the sister-group clade to the Trichoptera + Lepidoptera clade (Hennig 1981, Kristensen 1981). The earliest Trichopteran fossil is the Lower Triassic form *Prophilopotamus asiaticus* Sukacheva from central Asia [**82**] (Fig. 79), which was assigned to the recent family Philopotamidae (Sukacheva 1973). Members of the Prorhyacophilidae, ancestral to the modern plesiomorphic family Rhyacophilidae (Sukacheva 1978, Shields 1988), are found in Upper Triassic strata of Australia [**79**]. During the Jurassic, diverse trace-fossils of caddisfly cases, resembling the constructional configurations of modern forms, have been amply documented (Sukacheva 1978). Notably, by Early Jurassic times, the first

FIGURE 79. Geochronologic history of the Haustoriate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Ross (1967), Sukacheva (1982) and Botosaneanu and Wichard (1983). The level of taxonomic analysis is the family; some families without fossil representatives are omitted. The outgroup is Lepidoptera. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.


MYA
($x10^6$)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
HAUSTORIATE MOUTHPARTS
Calamoceratidae
Leptoceridae
Helicopsychidae
Molannidae
Odontoceridae
Sericostomatidae
Beraeidae
Vitimotaulidae
Brachycentridae
Goeridae
Limnephilidae
Lepidostomatidae
Baissoferidae
Phryganeidae
Dysoneuridae
Prorhyacophilidae
Hydroptilidae
Hydrobiosidae
Glossosomatidae
Rhyacophilidae
Necrotaulidae
Stenopsychidae
Philopotamidae
Polycentropidae
Hydropsychidae
Psychomyiidae
Electalbertidae
LEPIDOPTERA
See Fig.85
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
?
49
50
51
52
53
54

demonstrable lepidopteran enters the fossil record [69] (Whalley 1985), indicating presence of the Lepidoptera as a sister-group. By the Early Cretaceous, several modern families are documented, including the Calamoceratidae and Leptoceridae in Australia [53], showing an indistinct head consistent with haustoriate mouthparts (Jell and Duncan 1986) and phryganeids in Transbaikalia [52] (Sukacheva 1968). The Late Cretaceous includes the relatively apomorphic Sericosomatidae from Taimyr amber of Siberia [37] (Zherikin and Sukacheva 1973, Sukacheva 1978) and an unnamed modern form from Canadian amber [35] (McAlpine and Martin 1969). Clearly, trichopterans originated by the Early Triassic and represented a diversity of at least several modern families by the close of the era.

A difficulty in the above pattern is the taxonomic affinity of several Late Permian to Early Cretaceous families which have been included in the Trichoptera by some (Martynova 1961, Sukacheva 1978, Hong 1983) but are excluded from the order by others (Hennig 1981). These families include the Permian Microptysmatidae, the Triassic Cladochoristidae, the abundant and diverse Jurassic to Cretaceous Necrotaulidae and the similarly aged Dysoneuridae. Wing venation in these mostly Mesozoic families are consistent with either a trichopteran or amphiesmenopteran affinity or, in the Permian group, a mecopteran affinity (Hennig 1981). Historically these families have been assigned to any of these three orders or have been accorded the separate ordinal status of the Paratrichoptera (Brues et al. 1954). From the few fossil body impressions that are available (e.g. Hong 1983, fig. 25d), it is difficult to discern haustoriate mouthparts. Tentatively, these families are considered as possible but unproven haustoriates.

Previous Designations. Haustoriate mouthparts rarely have been recognized as a distinct type. During the early 1800's they were considered as part of the high-level taxon, "Mandibulata," by Clairville (1798-1806) and Stephens (1828). Trichopterans were not mentioned in the discussions of mouthpart morphology by Metcalf (1929) or James and Harwood (1969) (Table 6). Smith (1985), in a functionally-based classification of insect mouthparts, included haustoriate mouthparts together with labellate, glossate and siphonate mouthparts into a category he termed "feeding on free liquids." Recently, Chaudonneret (1986) considered both haustoriate and siphonate mouthparts as variations of his mouthpart structure theme, "*pièeces buccales lecheuses*."

Clarification of the term **haustoriate** to refer to this mouthpart class is important. Traditionally, the fleshy hypopharyngeal structure of trichopterans has been designated as a "haustellum" (Crichton 1957, Matsuda 1965, Denis and Bitsch 1973). However, the term "haustellum" also refers to the labially-derived structure ensheathing mouthpart stylets and contributing to the formation of the beak or mouthcone in hemipteroids and the proboscis in dipterans and siphonapterans. To eliminate confusion involving two distinct uses of the same term, I am supressing usage of the term "haustellum" and substituting the new term "haustorium" to refer to any fleshy, pseudotracheate, projecting hypopharynx (see Section 8.1.4).

Review of the Literature. The seminal paper detailing mouthpart structure for adult trichopterans is Crichton's (1957) study, wherein he includes an analysis of the hypopharynx microstructure and structural head and mouthpart variation within commonly recognized trichopteran families. Supplementing Crichton's extensive study is Klemm's (1966) examination of the structure and function of *Rhyacophila septentrionis* MacLachlan. Publications detailing head and mouthpart structure for several trichopteran genera include Ulmer's (1905) brief review of the group, Deoras' (1943, 1944) descriptions of genera from several Eurasian families, Durand's (1955) description of species from families occurring in France, and Mosely's (1936) and Neiboss' (1977) monographs on various relatively unknown Tasmanian caddisflies. Incidental accounts of particular trichopteran species, most of them exotic forms not treated by Crichton (1957), include Döhler (1915) for the bizarre stenopsychid *Pseudostenospyche sugens* Döhler; Anderson and Lawson-Kerr (1977) for the unusual marine commensal of echinoderms, the chathamiid *Philansius plebius* Walker; Riek (1968b) for the Tasmanian *Tasimia natasia* Mosely; Lucas (1893) for the limnephilid *Anabolia furcata* Lucas; Cummings (1914a) for the unique, elongate proboscis of the plectrotarsid *Plectrotarsus gravenhorstii* Kolenati; Cummings (1914b) for description of the unusual maxillary palpi of the sericostomatid *Sericostoma personatum* (Spence); and Korboot (1964) for the leptocerid *Triplectides volda* (Mosely).

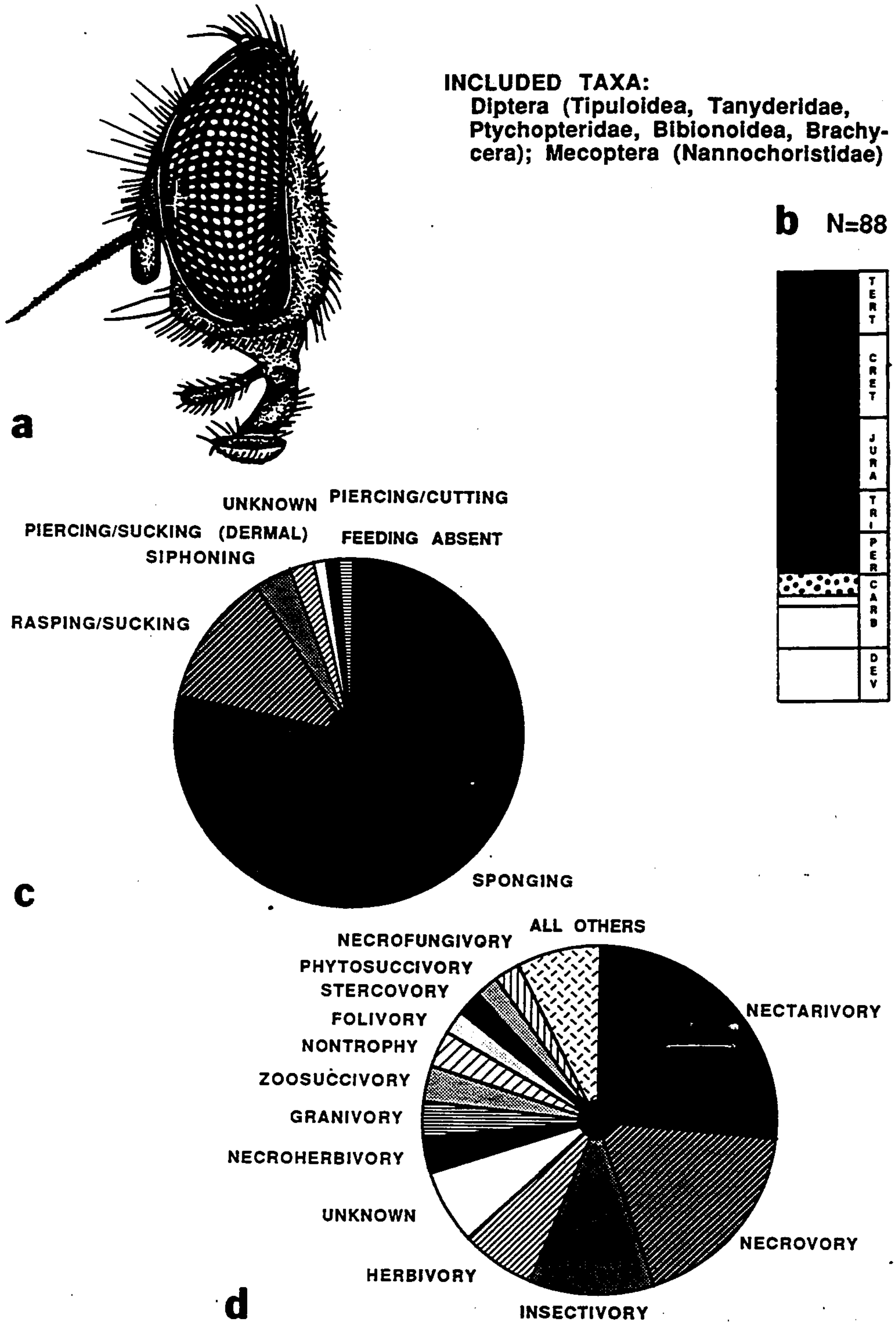
8.5.3. Labellate Class
(Class 17)

Description. Head spheroidal; retractile; with a long (rarely short) proboscis. Genae and gula well developed, infrequently moderately to minimally developed. Antennae aristate, infrequently setaceous or filiform; ocelli 3, rarely absent; compound eyes expansive, generally dichoptic. Mouthparts labellate; hypognathous; symmetrical; retractile. Food pump clypeal and pharyngeal.

Clypeus quadrate; fused to frons. Labrum vertically elongate, rarely quadrate; divided into 2 sclerites or undivided; margin acute or acuminate. Pharynx modest; hypopharynx a chitinized, bulbous reservoir with an apertuate lobe, or rarely stylate or fimbriate; epipharynx membranous or rarely setate. Mandibles absent. Maxillary main-body of 2 sclerites; stipes elongate; bearing a lacinia and palpus, occasionally bearing a palpus only. Maxillary palps filiform and clavate, often penicillate. Lacinia palpiform when present. Labial main-body equant to elongate, of 2 segments; bearing palps only. Labial palps 2-segmented; conjoined into a fleshy, distally expanded labellum; distal surface pseudotracheate and often denticulate; short to intermediate in length. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. Several features are restricted to the labellate class, the most prominent of which is the distinctive, prominent labellum. The labellum is an enlargement of the medially fused, labial palps that have expanded ventrally to form a fleshy, pseudotracheate, nondentate sponging organ. The gula proper, mandibles, and labial palp analogs are absent. While the ocellar tubercle with triangularly-positioned ocelli is not unique, it is only present in labellostylates and possibly a few stylate-haustellate forms among other mouthpart classes. Although not occurring in all members of the class, labellates are the only mouthpart class to have the unique, lever-based, retractile proboscis that can be collapsed into a ventral subcranial cavity when not in use.

Diversity and Natural History. Labellates are one of the dominant, conspicuous components occupying fluid-feeding guilds in terrestrial habitats. They comprise approximately 113 families, 5,670 genera and 71,800 species (Appendix D) and have a rank-order of 7 out of 34 mouthpart classes (Table 5, Fig. 131). They have a specieswise representation of 10% in the recent hexapod fauna. With the exception of a few groups that abrade skin, labellates are unable to penetrate biological integuments and must rely on exposed surface fluids or small particles for food. Although fluid feeding places a limitation on the consistency of ingested food, labellates nevertheless consume the entire spectrum of fluid food types. They consume animal fluids (honeydew, blood, serum, sweat and urine), plant fluids (guttated sap, resins, nectar, oils), fungal fluids (deliquescing hymenia, intracellular fluids), fluidized decomposing materials (carrion, rotting vegetable matter of diverse kinds, dung) as well as small-particulate matter (pollen, spores) in the 20 to 40 micron range (Fig. 80). Apparently, labellates are the dominant consumers of exposed surface fluids in most terrestrial habitats, nectar excepted (Willemstein 1987). Finally, since labellates consist almost entirely of dipterans lacking stylate



INCLUDED TAXA:
Diptera (Tipuloidea, Tanyderidae, Ptychopteridae, Bibionoidea, Brachycera); Mecoptera (Nannochoristidae)

FIGURE 80. Overview of the Labellate Mouthpart Class. a, *Fannia subpellucens* (Zetterstedt) (Diptera: Muscidae, data-set no. 993); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

mouthparts, they comprise one of the four major pollinator groups of angiosperms. However, unlike siphonate and glossate pollinators, labellates have modified their mouthparts considerably and consequently possess a wider anthophilous and nonanthophilous dietary repertoire than their fellow obligate anthophiles.

Plant-associated labellates comprise about 70% of the class and are taxonomically distributed unevenly throughout the class. Within this grouping, anthophilous forms constitute the overwhelming majority of species. For example, among Australian dipterans, 51% of all species of anthophilous (Armstrong 1979), virtually all of which are labellates. The importance of labellates in angiosperm pollination was recognized by Proctor and Yeo (1973) and Faegri and van der Pijl (1980), who described structural features of certain flower types that were dominately pollinated by labellate flies. The two syndromes representing these features are termed the fly blossom syndrome, or myiophily, and the carrion fly blossom syndrome, or sapromyiophily (Faegri and van der Pijl 1980, Wyatt 1983). Fly blossoms are characterized by radially symmetrical, simple, small flowers that lack significant depth appearance and bear dull, light colors. Sexual organs are well-exposed, odor is weak, and nectar is generally easily obtained by conspicuous floral markings, or nectar-guides (Baker and Hurd 1968, Faegri and van der Pijl 1980, Willemstein 1987). Fly blossoms are a diverse suite of flowers of mostly herbaceous families with small, broad and tubular flowers that includes genera such as *Trifolium* (clover), *Saxifraga* (saxifrage), *Achillea* (yarrow), *Euphorbia* (spurge) and *Mentha* (mint) for the European flora (Procter and Yeo 1973). They are pollinated by a diverse assemblage of mostly noncalyptrate flies, including Tipulidae (crane flies), Bibionidae (march flies), Cecidomyiidae (gall midges), Stratiomyiidae (soldier flies), Rhagionidae (snipe flies), Bombyliidae (bee flies), Phoridae (humpbacked flies), Syrphidae (hover flies) and Conopidae (thickheaded flies) and Calliphoridae (blow flies) (Proctor and Yeo 1973).

Of these, syrphids and bombyliids are first and second, respectively, in order of importance in many habitats (e.g. Herrera 1988). Syrphids have been documented as major pollination vectors in warm-temperate forest, cool-temperate forest and alpine communities in Japan (Yumoto 1986, 1987, 1988), as the dominant pollinators of the shrub *Lavandula* (lavender) in southern Spain (Herrera 1988) and are the most important labellate pollinator group in Australia (Armstrong 1979). Syrphids are also one of the few labellates that consume large quantities of pollen (Holloway 1976), using salivary secretions to procure dry pollen grains by incorporating them into a slurry that is ingested (Schumacher and Hoffman 1982). Syrphids also exhibit a partitioning of food resources since shorter-labellate syrphids tend to be pollinivorous whereas longer-labellate species were nectarivorous (Gilbert 1981). Bombyliids, like syrphids, are capable of hovering stationary over a flower but are obligately nectarivorous (Barth 1985). In eastern North America, bombyliids are a very effective specialized pollinator of *Hedyotis* (bluets) and are probably important pollinators for many other common spring herbs (Grimaldi 1988).

By contrast carrion fly blossoms contain radial pollination units that often have great depth, are surrounded by various traps and appendicular structures, and lack nectar (this and the following discussion is largely from Baker and Hurd 1968, Faegri and van der Pijl 1980, Willemstein 1987). Floral color ranges from subdued brown to burnt red to dark purple or even green, and the floral surface often appears mottled with a dull texture. Transparent windows occur on floral structures and emitted odors are strong, mimicing decaying meat, excrement or rotting vegetation. Carrion fly blossoms attract Sarcophagidae (blow flies), Scatophagidae (dung flies), Drosophilidae (pomace flies) and Mycetophilidae (fungus gnats), among others. Typical carrion flowers include *Symplocarpus* (skunk cabbage), *Sarracenia* (pitcher plant) and *Aristolochia* (birthwort), and reaches its greatest development in *Amorphophallus*, which produces an offensive stench from a flower two meters tall (Jolivet 1986).

In addition to the characterization of labellates by membership in either of the fly pollination syndromes, labellates can be either generalized or specialized pollinators. For example, some tabanids, bombyliids and nemestrinids possess short labella that feed on nectar from a wide selection of less-specialized flower species, whereas those with longer proboscides (up to 5cm long) feed on deep-throated gullet flowers that are also pollinated by siphonates (Proctor and Yeo 1973). Some labellates are highly specific with regard to the plants they pollinate, such as monospecific labellate pollinators of various tropical orchids.

Finally, whereas most labellates are anthophilous, many others, particularly many calpytrate and some acalyptrate muscoids, rarely frequent flowers and subsist on various decaying or fermenting products.

These substances include fluids produced by carrion, dung and rotting fruit which are sponged in a similar manner as nectar on anthophilous forms (Oldroyd 1964).

Little is known of the life-history or diet of the secretive Nannochoristidae. Their natural history was not discussed in a review of mecopteran feeding habits by Carpenter (1931). There is a hint that, like many other mecopterans, that they may be necrovores (Richards and Davies 1977).

Structural Themes. Labellate mouthparts are categorized into 11 fundamental themes, indicated by the subclustering patterns in Fig. 81. Because of the highly stereotyped nature of the maxillae and labrum and the absence of mandibles, the principal characters that are primarily responsible for subcluster formation are those of the sensory organs, general features of the mouthparts, labrum and pharyngeal region. The 10 characters accounting for most of the subcluster formation are rostrum/proboscis development, antennal type, ocellar number, mouthpart placement on the head capsule, mouthpart basic type, food pump type, labral subsegmentation, hypopharynx type, labial palp type and labial participation in a multielement mouthpart structure (see Appendix A). structural themes.

The subclustering patterns of labellate mouthparts consists of a taxonomically diverse central subcluster that is surrounded by significantly less structured subclusters. Some of these peripheral subclusters are monotaxic and include the primitive nematoceran groups Tipuloidea and Psychodoidea. Subcluster 1 (bracketed in Fig. 81 by data

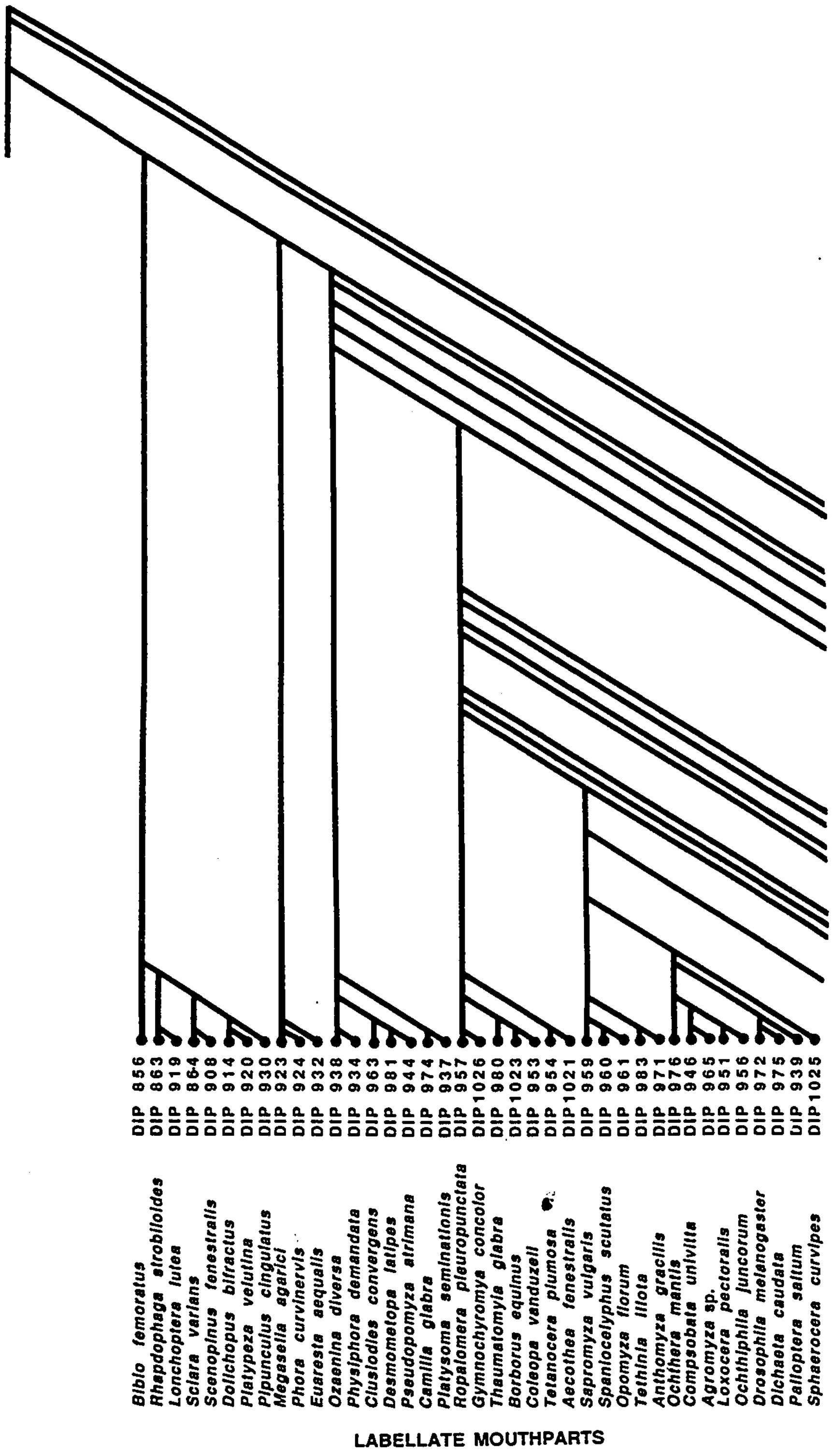
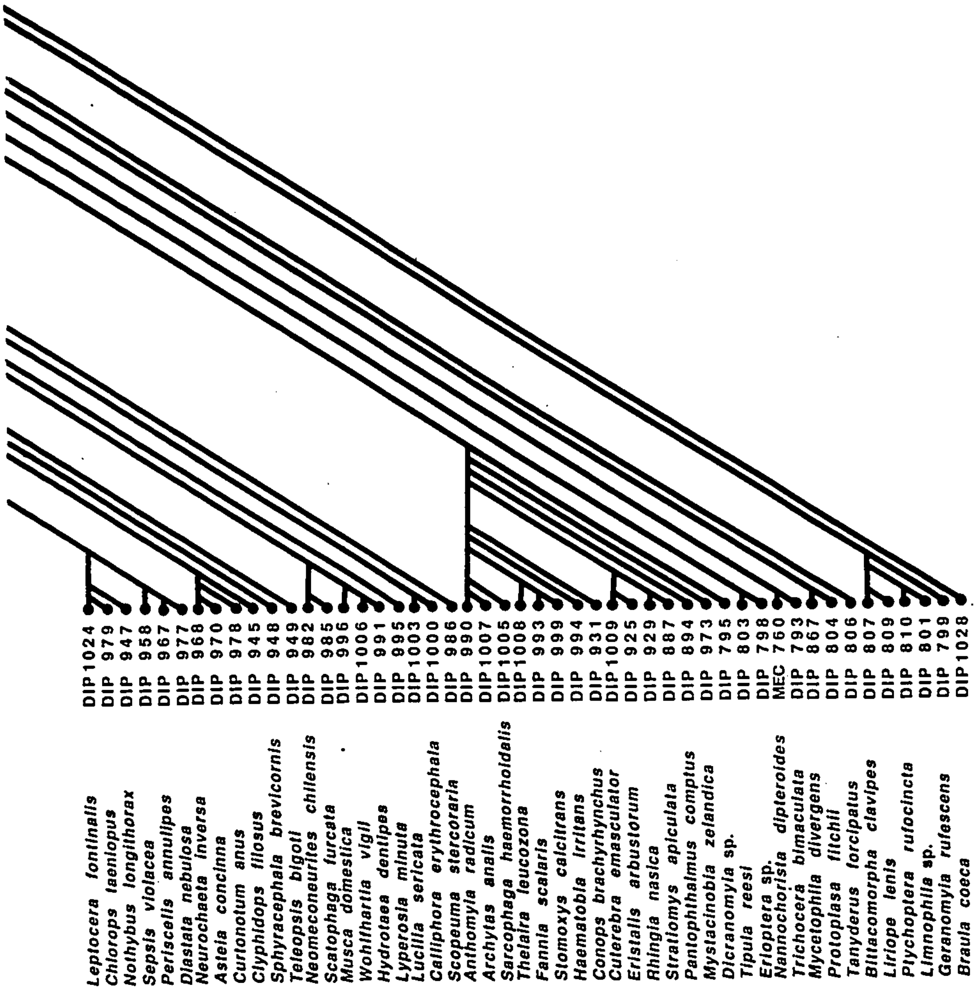

DIP 856 Bibio femoratus
DIP 863 Rhapdophaga strobiloides
DIP 919 Lonchoptera lutea
DIP 864 Sciara varians
DIP 908 Scenopinus fenestralis
DIP 914 Dolichopus bifractus
DIP 920 Platypeza velutina
DIP 930 Pipunculus cingulatus
DIP 923 Megaselia agarici
DIP 924 Phora curvinervis
DIP 932 Euaresta aequalis
DIP 938 Ozaenina diversa
DIP 934 Physiphora demandata
DIP 963 Clusiodes convergens
DIP 981 Desmometopa latipes
DIP 944 Pseudopomyza atrimana
DIP 974 Camilla glabra
DIP 937 Platysoma seminationis
DIP 957 Ropalomera pleuropunctata
DIP1026 Gymnochyromya concolor
DIP 980 Thaumatomyia glabra
DIP1023 Borborus equinus
DIP 953 Coleopa vanduzeii
DIP 954 Tetanocera plumosa
DIP1021 Aecothea fenestralis
DIP 959 Sapromyza vulgaris
DIP 960 Spaniocelyphus scutatus
DIP 961 Opomyza florum
DIP 983 Tethinia illota
DIP 971 Anthomyza gracilis
DIP 976 Ochthera mantis
DIP 946 Compsobata univitta
DIP 965 Agromyza sp.
DIP 951 Loxocera pectoralis
DIP 956 Ochthiphila juncorum
DIP 972 Drosophila melanogaster
DIP 975 Dichaeta caudata
DIP 939 Psilloptera saltum
DIP1025 Sphaerocera curvipes
LABELLATE MOUTHPARTS

FIGURE 81. Cluster analysis dendrogram of taxa comprising the Labellate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

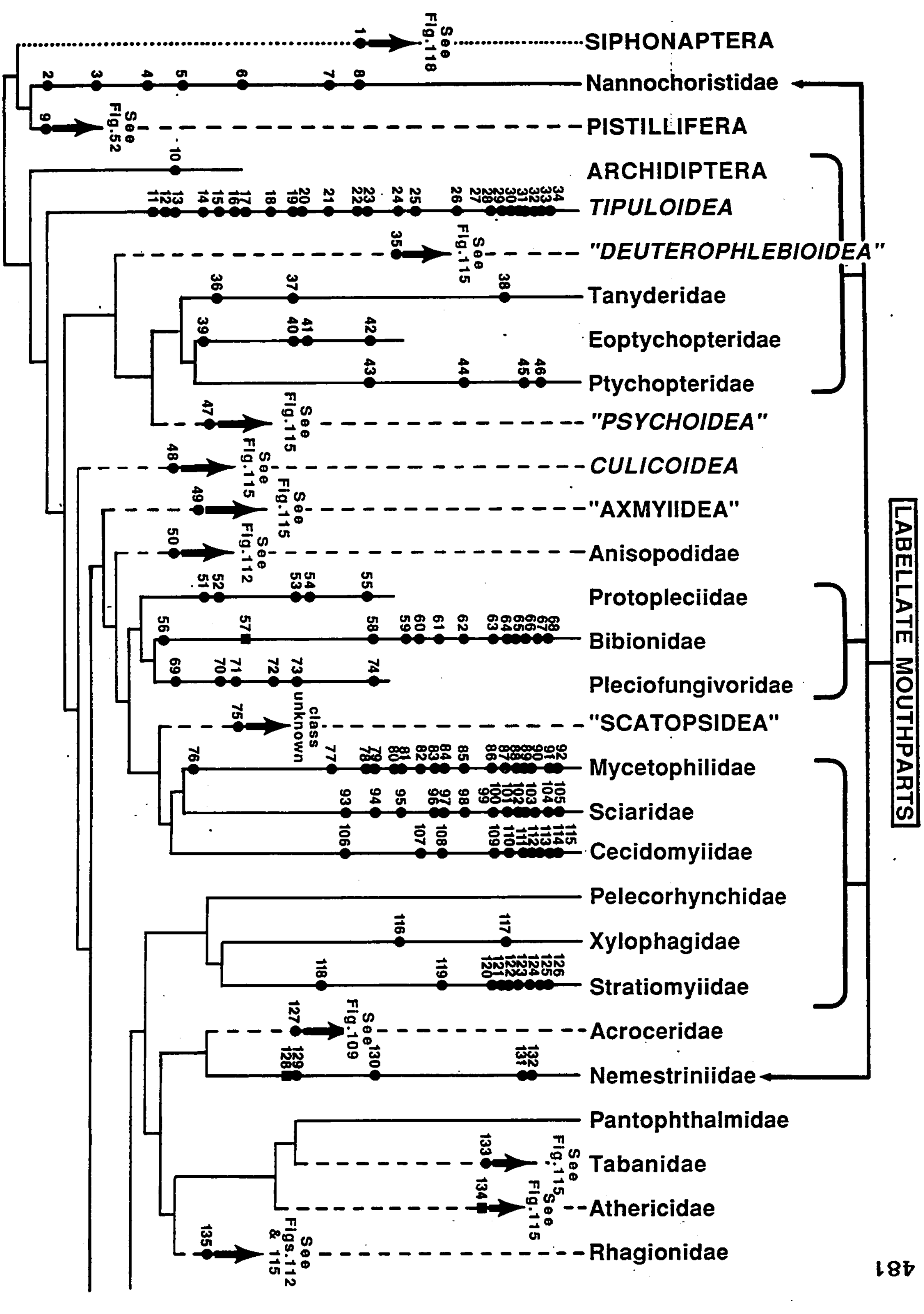

Leptocera fontinalis DIP1024
Chlorops taeniopus DIP 979
Nothybus longithorax DIP 947
Sepsis violacea DIP 958
Periscelis annulipes DIP 967
Diastata nebulosa DIP 977
Neurochaeta inversa DIP 968
Asteia concinna DIP 970
Curtonotum anus DIP 978
Clyphidops filosus DIP 945
Sphyracephala brevicornis DIP 948
Teleopsis bigoti DIP 949
Neomeconeurites chilensis DIP 982
Scatophaga furcata DIP 985
Musca domestica DIP 996
Wohlfhartia vigil DIP1006
Hydrotaea dentipes DIP 991
Lyperosia minuta DIP 995
Lucilia sericata DIP1003
Calliphora erythrocephala DIP1000
Scopeuma stercoraria DIP 986
Anthomyia radicum DIP 990
Archytas analis DIP1007
Sarcophaga haemorrhoidalis DIP1005
Thelaira leucozona DIP1008
Fannia scalaris DIP 993
Stomoxys calcitrans DIP 999
Haematobia irritans DIP 994
Conops brachyrhynchus DIP 931
Cuterebra emasculator DIP1009
Eristalis arbustorum DIP 925
Rhingia nasica DIP 929
Stratiomys apiculata DIP 887
Pantophthalmus comptus DIP 894
Mystacinobia zelandica DIP 973
Dicranomyia sp. DIP 795
Tipula reesi DIP 803
Erioptera sp. DIP 798
Nannochorista dipteroides MEC 760
Trichocera bimaculata DIP 793
Mycetophila divergens DIP 867
Protoplasa fitchii DIP 804
Tanyderus forcipatus DIP 806
Bittacomorpha clavipes DIP 807
Liriope lenis DIP 809
Ptychoptera rufocincta DIP 810
Limnophila sp. DIP 801
Geranomyia rufescens DIP 799
Braula coeca DIP1028

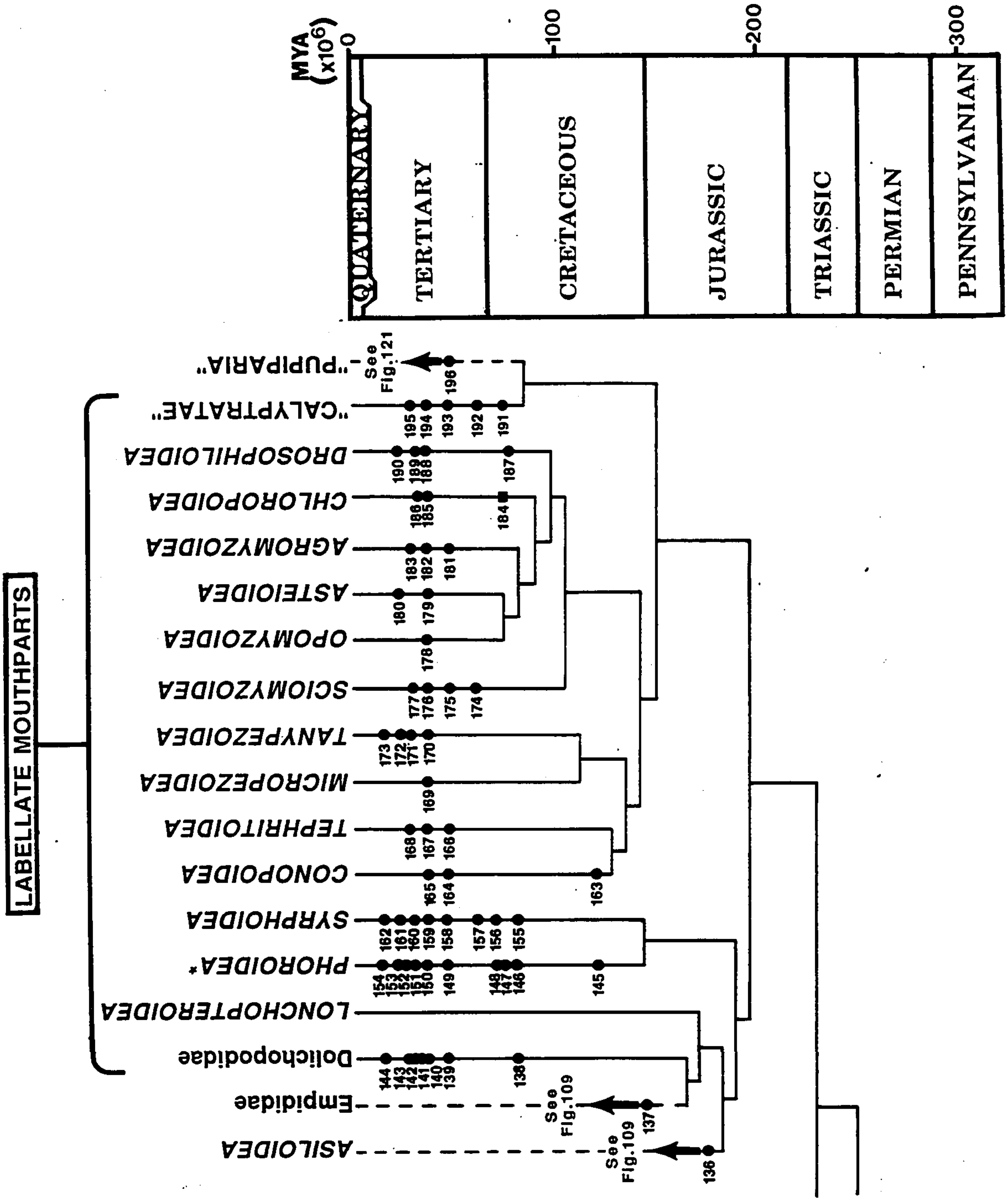
LABELLATE MOUTHPARTS

set nos. 856 to 930) consists of apomorphic nematocerans (Bibionoidea), brachycerans (Asiloidea, Empidoidea) and plesiomorphic cyclorrhaphans (Lonchopteroidea, Phoroidea and Syrphoidea). This group represents a plesiomorphic labellate facies in which the lever-based labellum retraction mechanism is absent or poorly developed. Subcluster 2 consists of three taxa (data-set nos. 923 to 932) of plesiomorphic cyclorrhaphans (Phoroidea and Tephritoidea). Subcluster 3 contains psychodoid nematocerans and five superfamilies of schizophoran cyclorrhaphans. By far the most taxonomically diverse assemblage of taxa is found in Subcluster 4 (957 to 986), characterized by 42 cyclorrhaphan taxa from 33 families of 11 plesiomorphic to apomorphic superfamilies. This central subcluster expresses the "typical" labellate condition of a distally fleshy, expanded, pseudotracheate labellum with a retraction mechanism. Subcluster 5 is a moderately diverse group comprising a few tipuloid nematocerans, tabanoid brachycerans and syrphid and conopoid cyclorrhaphans. However it importantly includes muscoid cyclorrhaphans that possess retractile pseudotracheate and denticulate labella. Subclusters 6 to 11 are peripheral, isolated groupings, each with one to at most a few constituent taxa. Subcluster 6 consists of the tipuloid taxa *Tipula reesi* (803) and *Erioptera* sp. (798), whereas Subcluster 7 consists of the tipuloid *Trichocera bimaculata* (793) and the plesiomorphic mecopteran *Nannochorista dipteroides* (760), which has a haustorium structurally convergent with the dipteran labellum. Subcluster 8 has the unusual combination of plesiomorphic and apomorphic nematocerans--the psychodid tanyderid *Protoplasa fitchii* (804) and the bibionoid mycetophilid *Mycetophila divergens* (867). Subcluster 9 consists of the nematoceran tanyderid *Tanyderus forcipatus* (806). Subcluster 10 displays the co-occurrence of five taxa of tipuloid and psychodoid nematocerans (807 to 799). Finally, the isolated Subcluster 11 accomodates the enigmatic braulid *Braula coeca* (1028), of unknown systematic affinity and an iniquiline inhabitant of colonial bee nests.

Geochronologic History. The fossil history of labellates chronicles the rise of one of the dominant insect groups that is coevolved with vascular plants. However, the earliest documented labellates precede the first angiosperms by 100 million years, indicating that preanthophilous species consumed fluid foods from other sources (Downes and Dahlem 1987). Consequently, much of the work on the intimate relationships between labellates and angiosperm pollination (Proctor and Yeo 1973, Faegri and van der Pijl 1980 and references therein) are inapplicable to Triassic, Jurassic and some Early Cretaceous forms. Available data indicate that fleshy, distally-expanded, labial palps, with or without pseudotracheae, but nevertheless capable of fluid food adsorption are plesiomorphous within the Diptera (Hennig 1981, but see Downes 1958). Accordingly, both nematoceran stylate mouthparts and the unique lever-based labellum of the Brachycera are apomorphous. These feeding-related aspects of Mesozoic dipteran evolution--presence of a fleshy labium for fluid feeding and absence of nectar produced by angiospermous plants--has led Downes and Dahlem (1987) to propose that preanthophilous dipterans derived their metabolically essential energy for flight from the only major available sugar-rich fluid available, aphid honeydew.

FIGURE 82. Geochronologic history of the Labellate Mouthpart Class. The continuation of this phylogram is on the next page. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after McAlpine and Martin (1966), Matile (1981), Hennig (1981), McAlpine and Wood (1989) and Willmann (1987). The level of taxonomic analysis is the superfamily for those superfamilies comprising only labellate taxa for the adult stage, or the family for those superfamilies comprising labellates and other mouthpart classes for the adult stage. Nothing is known of the mouthparts of the suborder Archidiptera. *Ironomyiid phoroids are distylate/tetrastylate. The outgroup is Siphonaptera. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.


SIPHONAPTERA
1
See Fig.118
Nannochoristidae
2 3 4 5 6 7 8
PISTILLIFERA
9
See Fig.52
ARCHIDIPTERA
10
TIPULOIDEA
11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34
"DEUTEROPHLEBIOIDEA"
35
See Fig.115
Tanyderidae
36 37 38
Eoptychopteridae
39 40 41 42
Ptychopteridae
43 44 45 46
"PSYCHOIDEA"
47
See Fig.115
CULICOIDEA
48
See Fig.115
"AXMYIIDEA"
49
See Fig.115
Anisopodidae
50
See Fig.112
Protopleciidae
51 52 53 54 55
Bibionidae
56 57 58 59 60 61 62 63 64 65 66 67 68
Pleciofungivoridae
69 70 71 72 73 74
"SCATOPSIDEA"
75
class unknown
Mycetophilidae
76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92
Sciaridae
93 94 95 96 97 98 99 100 101 102 103 104 105
Cecidomyiidae
106 107 108 109 110 111 112 113 114 115
Pelecorhynchidae
Xylophagidae
116 117
Stratiomyiidae
118 119 120 121 122 123 124 125 126
Acroceridae
127
See Fig.109
Nemestriniidae
128 129 130 131 132
Pantophthalmidae
Tabanidae
133
See Fig.115
Athericidae
134
See Fig.115
Rhagionidae
135
See Figs.112 & 115
LABELLATE MOUTHPARTS


MYA
(x10^6)
0
100
200
300
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
PENNSYLVANIAN
LABELLATE MOUTHPARTS
"PUPIPARIA"
See Fig.121
196
"CALYPTRATAE"
195 194 193 192 191
DROSOPHILOIDEA
190 189 188 187
CHLOROPOIDEA
186 185 184
AGROMYZOIDEA
183 182 181
ASTEIOIDEA
180 179
OPOMYZOIDEA
178
SCIOMYZOIDEA
177 176 175 174
TANYPEZOIDEA
173 172 171 170
MICROPEZOIDEA
169
TEPHRITOIDEA
168 167 166
CONOPOIDEA
165 164 163
SYRPHOIDEA
162 161 160 159 158 157 156 155
PHOROIDEA*
154 153 152 151 150 149 148 147 146 145
LONCHOPTEROIDEA
Dolichopodidae
144 143 142 141 140 139 138
Empididae
See Fig.109
137
ASILOIDEA
See Fig.109
136

The earliest known fossil labellates are nannochoristid mecopterans, including *Cyclochorista convexicosta* Martynova from the Kusnetsk Basin of the USSR [97] (Martynova 1958, 1961) (Fig. 82). Nannochoristids are one of the oldest families of insects and their sister-group, Diptera (Kristensen 1981, Willmann 1989), includes primitively labellate taxa among tipuloid and bibionoid nematocerans (Fig. 82). Among dipterans there is the tendency toward fluid-feeding occurred in parallel for both the larval and adult stages. Much of the labellate class is taxonomically congruent with the mouthhook class since they are adult and larval expressions of the same taxa. Since much of the geochronologic history of the mouthhook and labellate mouthpart classes occurred in tandem and the same fossil specimens can be used to affirm directly or indirectly the presence of either mouthpart class at a given time, I have attempted to minimize overlap with Section 8.4.4.

Labellates are relatively well represented in Mesozoic deposits when compared to other insect groups and much of their fossil presence is based on wings, since soft-body preservation of poorly sclerotized dipterans is uncommon in Triassic to Lower Cretaceous strata. Although the Lower Triassic form "*Pseudodiptera gallica*" Laurentiaux and Grauvogel was originally assigned to the Diptera based on wing venation and presence of a much reduced hindwing, it subsequently has been assigned to the Mecoptera (Rohdendorf 1974) or Paratrichoptera (Hennig 1981), both of which are stem-groups in the ancestry of the Diptera. Apparently the earliest known dipteran is the Upper Triassic tipulid *Architipula* *radiata* Rohdendorf from the USSR [73] which, in some ways, is more advanced in wing venation than many extant tipulids (Hennig 1981). If Hennig's assessment of the derived nature of the wing venation of *Architipula* is correct, then it is highly likely that *Architipula* also bore labellate mouthparts. *Architipula* is herein considered the earliest member of the Labellate Class. From the same deposit, Rohdendorf assigned six other forms to the Suborder Archidiptera, a designation given some support by Carpenter and Burnham (1985) but rejected by Hennig (1981), who does not considers them as dipteran.

Bibionoid dipterans are another group of labellates that are recorded from the Upper Triassic and are associated with numerous co-occurring stylate-haustellate dipteran taxa (Rohdendorf 1974, Kalugina and Kovalev 1985). Forms such as *Protobliogaster rhaetica* Rohdendorf probably belong to the stem group of the Bibionoidea. Notably, some bibionoids such as mycetophilids (fungus gnats) are pollinators of nonangiospermous plants (Brecton and Ortiz 1985).

Orthorrhaphan brachyceran dipterans belonging to the Tabanoidea such as the Rhagionidae (snipe flies) are known from the Lower Jurassic [67] (Rohdendorf 1974; Kovalev 1981, 1985) and forms belonging to the sister-group of the exclusively labellate Brachycera are present in the Upper Triassic [73], indicating the occurrence of plesiomorphous brachycerans among some of the earliest known dipterans (Hennig 1981). The earliest brachyceran, *Palaeobrachyceron* Kovalev from the Early to Middle Jurassic of Transbaikalia, USSR [66], is assigned to the extant family Rhagionidae and bears a well-developed labellate proboscis

(Kovalev 1981, fig. 1; 1982), although it is short and unlike the longer proboscides of many Tertiary forms (Zaitzev 1981). However, nemestrinids (tanglewing flies) described from the Upper Jurassic of the USSR [60] apparently bore long proboscides (Rohdendorf 1968), indicating fluid feeding of fluids in inaccessible structures. During the Jurassic, orthorrhaphan groups, including stratiomyoids (Hong 1983), asiloids (Usachev 1968, Kalugina and Kovalev 1985) and bombyloids (Kalugina and Kovalev 1985) were locally abundant.

During the Cretaceous there was a continued diversification of orthorrhaphans, particularly bombyliids (Zaitzev 1981), and various new cyclorrhaphan groups such as platypezids [55] (Hennig 1971), sciomyzids [56] (Whalley and Jarzembowski 1985) and probable drosophiloids [53] (Jell and Duncan 1986). This expansion of labellates increased during the Late Cretaceous and is represented by empidids from France [45] (Schlüter 1978, Negrobov 1978) and Botswana [43] (Waters 1988a,b), syrphids and sciadocerids from Siberia [37] (Zherikin and Sukacheva 1973, Kovalev 1985), and ironomyiids, chlorpoids and calliphorids from Canada [35] (McAlpine and Martin 1969; McAlpine 1970, 1973). The apparent diversification of these nectarivorous, pollinivorous and necrovorous labellates parallel the radiation of Late Cretaceous flowering plants, suggesting that numerous coevolving relationships were being established. In a survey of angiosperm/insect pollination during the Late Cretaceous, Crepet and Friis (1987) indicate that by the Cenomanian, fly-pollinated flowers with large floral discs and probable nectaries (e.g. Rhamnaceae) were present, followed later by smaller, simpler unspecialized flowers during the Turonian and Campanian and, by Maestrichtian times, the appearance of zygomorphous myiophilous flowers (Myrtales) is evident. By the Early Tertiary there is a diversity of labellate families with proboscides similar to the recent fly fauna (Hennig 1965; Wilson 1978a,b; Larsson 1978), as well as the the presence of myiophilous and sapromyiophilous flowers from several deposits, such as the Middle Eocene Claiborne Formation of Tennessee [25] (Crepet 1979a,b). These data indicate that labellates were a major pollinator assemblage in at least some environments, much as they are today.

Previous Designations. The labellate mouthpart condition has been traditionally recognized in almost every study of insect mouthparts (Table 6). Aristotle considered flies as having a proboscis adapted to feeding on various fluid substances. Fabricius (1775, 1799) considered the Diptera as having sucking mouthparts with a fleshy, seta-bearing, unsegmented proboscis. Clairville (1806), MacLeay (1821) and Spence (1826) regarded dipterans as part of their formal, supraordinal taxon, "Haustellata."

During the modern era, Metcalf (1929) assigned dipterans to his "sponging type" within his Haustellate Series, a designation that was repeated by Metcalf, Flint and Metcalf (1962). James and Harwood (1969) considered the "dipteran mouthpart type" as a distinctive taxonomic-structural grouping and placed the house fly into his fourth subtype--a placement that is approximately congruent with my labellate condition. By contrast, Ross et al. (1982) and Smith (1985) focused on function and discussed dipteran mouthparts as "sponging types" and "feeding on free liquids" respectively (see Table 6). In a recent study Chaudonneret (1987) recognized the uniqueness of dipteran mouthparts under the heading "*l'appareil de quelques Diptères.*"

The labellum is the most distinctive mouthpart element of members of this mouthpart class. Consequently, I have borrowed the term **labellate** to refer to a mouthpart class consisting of forms bearing a sponging labellum.

Review of Literature. A considerable amount of literature has been devoted to description and interpretation of labellate mouthparts. Since dipterans among all hexapod orders bear the greatest diversity of adult mouthparts, synthetic, comparative studies of representative genera within the order have provided major challenges. The most commendable of these is McAlpine et al. (1981, 1987), whose two-volume compendium, *Manual of Nearctic Diptera*, provides excellent verbal and pictorial descriptions of head and mouthpart structure for every dipteran family occurring in North America. An earlier comprehensive summary is Peterson's (1916) detailed *The Head Capsule and Mouthparts of the Diptera*, in which members from 53 families of Diptera are figured. Briefer synthetic studies include Smith (1890), and Hu and Peng (1936), Crampton (1942) and Hoyt (1952).

Comparative studies focusing on particular families or groups of families are Frey (1913) for the Mycetophilidae, Sciaridae and Cecidomyiidae; Frey (1921) for the Schizophora; Cregan (1941) for the Dolichopodidae; and Aczel (1961) for the Neeriidae. Several studies examine head and mouthpart structure in selected species. Notable in this regard is Rees and Ferris' (1939) study of the tipulid *Tipula reesi* Alexander, Chassignard and Tsacas' (1974) examination of the rhagionidis *Chrysopilus auratus* Fabricius and *Vermileo vermileo* DeGeer, Zaitland and Larsen's (1984) SEM study of the mydid *Mydas clavatus* Drury, Bletchley's (1954) description of the empidid *Empis livida* Linneaus, Frew's (1923) work on the chloropid *Chlorops taeniopus* Meigen and lastly Bletchley's (1955) treatment of the scatophagid *Scopeuma stercoraria* (Linneaus).

More numerous are short treatments of head and mouthpart structure found in major taxonomic descriptions of selected species. A selected few include Hammond's (1874) examination of *Tipula* sp.; Williams' (1933) study of the tanyderid *Protoplasa fitchi* Osten Sachen; Gouin's (1958) description of the stratiomyiid *Chrysochroma bipunctum* Scopoli; McAlpine's (1967) description of the monotypic ironomyid *Ironomyia nigromaculata* White; Aczel's (1961) study of the nothybiid *Nothybus autumnalis* DeGeer; Chilcott's (1966) monograph of the Fanninae, emphasizing *Fannia scalaris* Robineau-Desvoidy; Suffolk's (1869) discussion of the proboscis of *Calliphora vomitoria* Linneaus; Kim and Cook's (1966) description of the sphaerocerid *Sphaerocera curvipes* Latreille; and Hassanein and Abd El-Salam's (1962) treatment of the enigmatic *Braula coeca* Nitsch.

Descriptions of the rare, adult nannochoristid *Nannochorista dipteroides* Tillyard are provided by Crampton (1921a, 1923b, 1942), Tillyard (1935), Hoyt (1952) and Hepburn (1969).

8.6. Siphonate Series

8.6.1. General Features of the Sipohonate Series

General Structure. Mouthparts of the Siphonate Series bear a prominent, elongate, tubular feeding organ, the siphon. Associated with the siphon is a powerful frontoclypeal pump borne on a generally transversely elongated head. The eyes are well-developed, large and frequently bulging. The mandibles are almost always supressed, although well-developed in coleopteran siphonomandibulates. The labrum ranges from well-developed to diminished, serving generally as a siphon brace. The nongaleal maxillae and labium are variously developed but always hypognathous. The lacinia is generally absent, rarely serving as a strygil for siphon grooming.

The galeal siphon is the key feature of the Siphonate Series. It consists of a central food canal formed by the conjoining of the right and left galeae by toothed hooks and/or overlapping, interlocking sclerites. The siphon is a flexible structure ranging from a short, truncate tube to a very long proboscis up to 25cm long (Kevan and Baker 1983). In almost all siphonates, the siphon is retractile by virue of spiral recoil upon relaxation of hemocoel pressure.

Included Classes. The Siphonate Series comprises the Siphonate and Siphomandibulate Mouthpart Classes. (See Table 5 for taxal membership, life-stages and number of taxa examined for each mouthpart class.)

Diversity and Other Distributional Patterns. The Siphonate Series is a moderately diverse mouthpart type in recent terrestrial ecosystems, serving an important role in the pollination of flowering plants. It comprises two classes and originated independently at least four times--once each in nonzeuglopteran lepidopterans, dipseudopsid trichopterans, the meloid coleopteran *Nemognatha* and at least two genera of rhipiphorid coleopterans. By virtue of the commonality of diet that siphonates share with glossates and many labellates, siphonates may be in competition with other mouthpart groups for the same food, specifically nectar. However, Baker and Baker (1980) and Kevan and Baker (1983) have presented evidence suggesting that the above nectarivorous groups partition nectar types according to nutritional quality, selecting nectars for viscosity and particular combinations of carbohydrates, proteins and lipids.

Siphonates imbibe sugar-rich foods, predominantly nectar, that is occasionally supplemented by protein in the form of pollen (Gilbert 1972, Common 1974). Members of this mouthpart class are major actors in the the pollination of flowers with a particular type of floral structure (Faegri and van der Pijl 1980). Flowers pollinated by siphonates characteristically bear deep, tubular corollas with well-hidden nectar in tubes or spurs (Wyatt 1983, Nilsson et al. 1987). Modifications of this basic syndrome exist for butterfly- and moth-pollinated flowers. The former consist of flowers bearing an erect corolla with fixed anthers and a flat rim serving as a landing platform for alighting butterflies. The latter differs by bearing a pendulous corolla, often with zygomorphic anthers, and dissected petals permitting pollination by hovering moths.

Major Structural Variations. The Siphonate Series is a morphologically well-integrated groundplan since all forms bear a suctorial siphon formed by conjoined galeae. However, two major mouthpart themes are expressed, based on the absence or presence of chewing mandibles. Functionally amandibulate mouthparts occur in the Siphonate Class, comprising vitually all nonzeuglopteran lepidopterans and dipseudopsid trichopterans. These forms feed entirely by siphoning fluids or fluid-particle suspensions.

The second major theme is the Siphonomandibulate Class, characterized by the handling and chewing of solid food as well as siphoning of fluid food. Members of this group are flower-frequenting coleopteran genera in the Meloidae and Rhipiphoridae. Although prominent mandibles suggest cantharophily, most evidence indicates that siphonomandibulates are dominately nectar-feeders and important pollinators (Barth 1985).

Geochronologic Range. Of all the mouthpart series, the Siphonate and Glossate Series are the most recently derived. The Siphonate Class appears to have originated by Early Cretaceous times and may have originated during the Jurassic (Skalsky 1979b, Whalley 1985). Whereas mandibulate zeuglopteran and zeuglopteran-like lepidopterans are known from Jurassic and Cretaceous shales (Skalski 1979a,b [52]; Rasnitsyn 1983, Whalley 1985 [69]) and Cretaceous and Eocene/Lower Oligocene ambers (Rebel 1935 [19]; Kühne et al. 1973; Schlüter 1974 [45]; Skalski 1976, 1979b; Whalley 1978, 1986 [55]), the earliest evidence for siphonates are possible nepticulid and lyonetid leafmines in the Upper Jurassic (Kozlov 1988, Rozefelds 1988) and demonstrable Upper (but not uppermost) body fossils from Cretaceous Siberian amber [37] (Skalski 1979b, Kozlov 1988). By Paleogene times, siphonates, including such derived forms as the Papilionoidea, were an established faunal element (Shields 1976, Durden and Rose 1978). Crepet (1983, 1984) has presented floral evidence for this conclusion based on pollination syndrome structures found on inflorescenses from Eocene deposits of the southeastern United States [25]. Although the evidence is fragmentary, siphonates probably coevolved with nectariferous angiosperms, although there is no reason to believe that they could not have been fluid-feeders during the Triassic or Jurassic. (See Crepet [1972, 1974] for discussions of cycadeoid pollination biology.) The history of the Sipohonomandibulate Class is less clear. Siphonomandibulates consist of two heteromeran cucujoid families, the Meloidae and Rhipiphoridae, the earliest record of which is Upper Eocene/Lower Oligocene Baltic amber [19] (Crowson et al. 1968, Abdullah 1975). Their origin probably occurred during the later Mesozoic.

8.6.2. Siphonate Class
(Class 19)

Description. Head spheroidal or transversely elongate, exserted from thorax; nonretractile; bearing a very long to rarely long proboscis. Genae minimally to well developed; gula minimally to moderately developed, often absent. Antennae setigerous, clavate or setaceous; ocelli absent, rarely 2; compound eyes expansive, dichoptic. Mouthparts siphonate, hypognathous, symmetrical, retractile. Food pump clypeal and pharyngeal.

Clypeus quadrate or transversely elongate; a single sclerite or fused to frons. Labrum vertically elongate, infrequently quadrate; undivided; margin a pilifer. Pharyngeal region modest; hypopharynx absent, rarely a bulbous reservoir; epipharynx forming ventral surface of food pump, or membranous or setate. Mandibles absent, rarely vestigial. Maxillary main-body of 2 sclerites; stipes elongate to infrequently quadrate; bearing a galea and palpus only. Maxillary palpus stubby or less often brustiate or filiform. Galeae conjoined into a double tubular siphon; laciniae absent. Labium with elongate to equant main-body of 1 sclerite; bearing labial palps only. Labial palps squamate or penicillate; 3-segmented; intermediate to long in length. Glossae and paraglossae absent. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. The combination of a well-developed galeal siphon and absence of mandibles, hypopharynx, laciniae, glossae and paraglossae is unique to the Siphonate Class. Additionally, the cranial capsule lacks an epicranial suture and the anterior aspect of the capsule consists of a flat, platelike and squarose frontoclypeal sclerite. The labium is frequently piliferate. Siphonate mouthparts are considerably modified, particularly by the absence of several mouthpart elements (*vide supra*). Such a condition is contrasted with siphonomandibulate mouthparts, which possess virtually all of the above missing elements and bear prominent, highly utilitarian mandibles (see Section 8.6.3).

Diversity and Natural History. With the possible exception of glossates (Sect. 8.7.2), siphonates are the mostly highly coevolved pollinator group among flowering plants. Like glossates but unlike labellates, virtually all siphonates that feed are associated with flowering plant nectar (Fig. 83), since their frequently long siphons are used to extract nectar and pollen that can not be retrieved by pollinators with shorter proboscides (labellates, most glossates, haustoriates, adult-ectognathates). The siphons of siphonates range from attenuated structures used as small sucking organs among some dacnonymphans, exoporians and monotrysans, to extremely elongate "tongues" in excess of 25 cm used by some ditrysans that pollinate certain Malagasy orchids (Nilsson et al. 1987). Many common ditrysan moths and butterflies bear siphons with a length around 0.5 to 3.0cm. Although anthophily is the dominant dietary theme of siphonates, other fluid foods are taken, including guttating sap, exuding liquids from fermenting fruit, aphid honeydew, dung, urine, mud/water suspension, fluidized carrion and even exposed blood (Proctor and Yeo 1973, Scott 1986). As in labellates, dry substances are also consumed by siphonates, and it is accomplished by ejection of fluid from the siphon or abdomen which liquifies the material that is subsequently imbibed (Scott 1986). Nevertheless, nectar is the principal diet of siphonates and its principal nutritive contribution to siphonate metabolism is sugar (Barth 1985). Nectar is generally about 20% by volume in most species of angiosperms, although a range from 9.3 to 49.5 % has been shown for a broad sampling of North American flowers (Cruden et al. 1983). Nectars

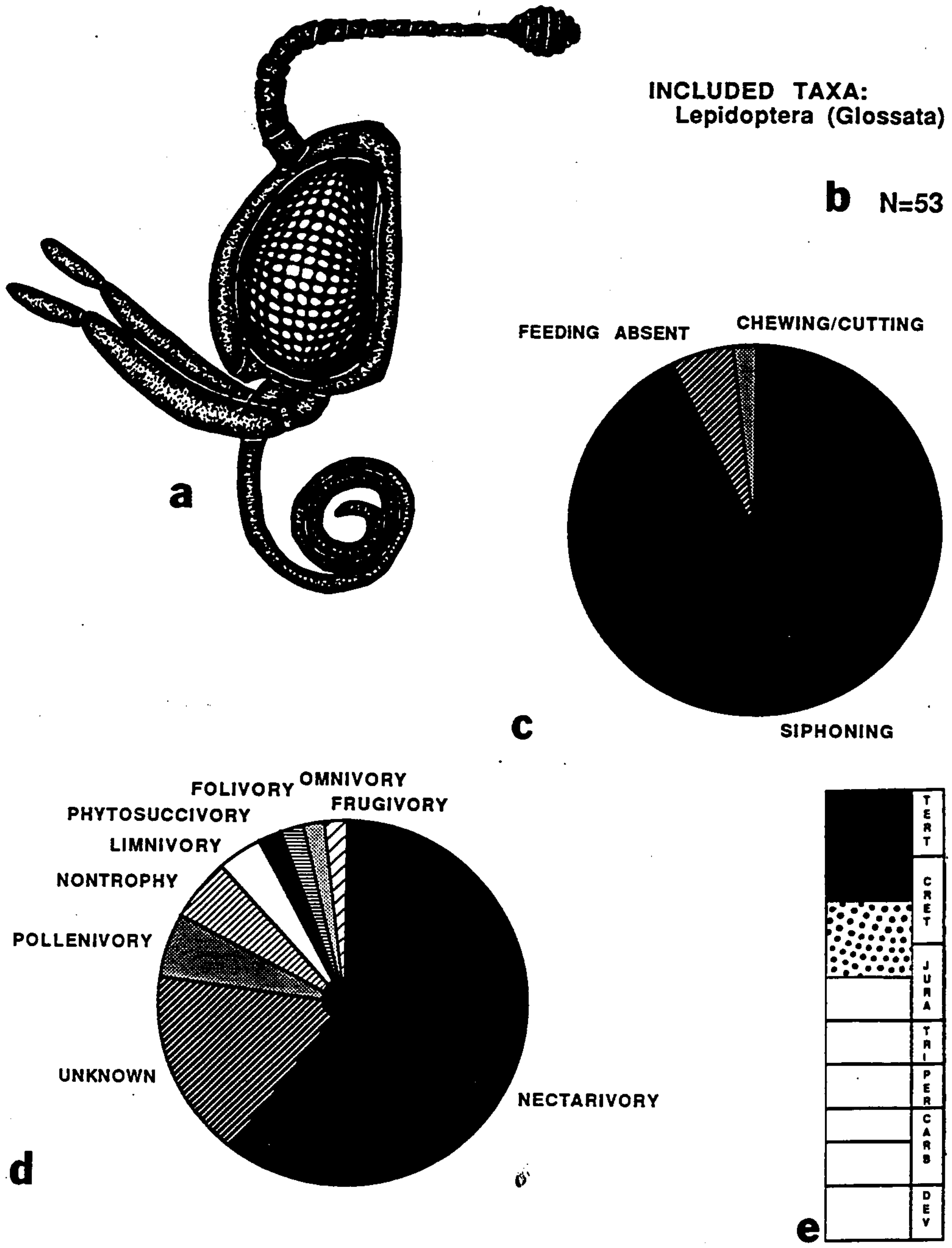


FIGURE 83. Overview of the Siphonate Mouthpart Class. a, *Sanninoidea exitosa* Fabricius (Lepidoptera: Sesiidae, data-set no. 1144); b, taxonomic distribution and number of taxa examined; c, functional-feeding-groups; d, dietary spectrum; e, geochronologic range.

also contain amino acids in varying but always substantially less concentrations than sugar (Baker and Baker 1983). Because of the hydrodynamic forces exerted by the diameters of their siphons, siphonates prefer diluter nectar solutions with sugars of lower molecular weight and abundant amino acids than do glossates (Scott 1986). In addition to nectar, other rewards have been suggested; Grant and Grant (1983) indicate that the presence of alkaloids in *Datura* (Solanaceae) constitutes an additional inducement for pollination by hawkmoths.

Siphonates are a taxonomically diverse and ecologically important group. They comprise 15.5% of all hexapods and have a diversity of 134 families, 14,450 genera and about 136,400 species (Appendix D), which translates to a rank-order of four among 34 mouthpart classes (Table 5, Fig. 131). Virtually all lepidopterans are included among siphonates, except for the primitively mandibulate zeuglopteran moths (Kristensen 1984b), several plesiomorphic groups of small moths lacking or bearing a rudimentary proboscis (Taylor 1957, Willemstein 1987) and several genera of sanguinivorous noctuid moths with piercing siphons (Bänziger 1971).

Because of the predominance of anthophily, several categories of pollination syndromes based on floral features have been ascertained for siphonates, similar to those for labellates and glossates. These syndromes are phlaenophily, or pollination by small moths and hawkmoths (sphingids), and psychophily or pollination by butterflies (Faegri and van der Pijl 1980, Wyatt 1983). Phlaenophilous flowers are nocturnally to crepuscularly-blooming, white to pale green in color, have a moderately strong and sweet scent, are actinomorphic and positioned horizontally or pendantly and produce concealed nectar without the benefit of nectar-guides. Psychophilous flowers bloom diurnally, are bright red, yellow or blue in color, produce a moderately sweet and strong scent, are typically actinomorphic with a deep and narrow tube or spur positioned upright and produce concealed nectar with the benefit of nectar guides. There are several structural and behavioral correlates of these pollination syndromes. Phlaenophilous flowers are pollinated by nocturnal or crepuscular moths that use odor for attraction to the flower and hover over the flower as they thrust their long siphons into a deep corolla or spur. By contrast, psychophilous flowers are pollinated mostly by diurnal butterflies (Papilionoidea) that are attracted to the flower by its bright colors and alight on the floral disc as they use their moderately long proboscis to probe for floral nectar (Faegri and van der Pijl 1980).

Some authors (Wyatt 1983) consider sphingophily, or pollination by hawkmoths, as a distinct pollination syndrome from phlaenophily. Grant (1983), for example, documented the prevalence of this pollination style for temperate North America. Because of the generally long siphon and avoidance of alighting by nocturnal sphingids, many flowers have developed extraordinary long corollar tubes or spurs to accommodate the pollinators (or vice versa). This phenomenon has been dramatically revealed by recent studies by Nilsson and coworkers (1985, 1987, 1988) for the Malagasy orchid *Angraecum* and its pollinator, the hawkmoth *Xanthopon*. In this system, nectar is produced at the base of a 28 to 32cm long spur of the orchid flower, such that pollination can only be effected if the hawkmoth uses its entire siphon to reach the nectar at the spur bottom and thus causing contact of the hawkmoth's head with viscid pollenia at the spur entrance. Thus, if the orchid floral spur was shorter or the hawkmoth siphon was longer, pollination could not occur, minimizing reproductive fitness of the orchid (Nilsson et al. 1987, 1988).

Although many examples of "sphingophily" and other modes of pollination constitute highly coevolved pollinator/host plant associations (Ehrlich and Raven 1964, Baker 1986), evidence indicates that the opposite pattern is at least prevalent. Herrera's (1988) study of *Lavandula* (lavender), a summer-flowering shrub in southern Spain, is a case in point. The pollinator fauna of the deep tubular flowers of *Lavandula* is taxonomically diverse and variable in space and time, with siphonates dominant near streams, glossates at dryer sites and long-proboscate labellates forming a substantial component at both sites. However, *Ladvandula* imposes severe morphological restrictions on mouthpart length for successful pollination to occur, resulting in the selection of a taxonomically heterogenous pollinator fauna with abilities to pollinate the shrub sequentially during the long flowering season. The effect of such a prolonged flowering season and relatively ephemeral pollinator species is to make pollinator/flowering plant specificity impossible.

Structural Themes. Siphonates are categorized into seven themes, each which is represented by a discrete subcluster (Fig. 84). Of these subclusters, Subclusters 4, 5 and 6 form the central core of siphonate mouthparts. Separation of these three central subclusters is principally attributed to differences in hypopharynx type, maxillary appendages

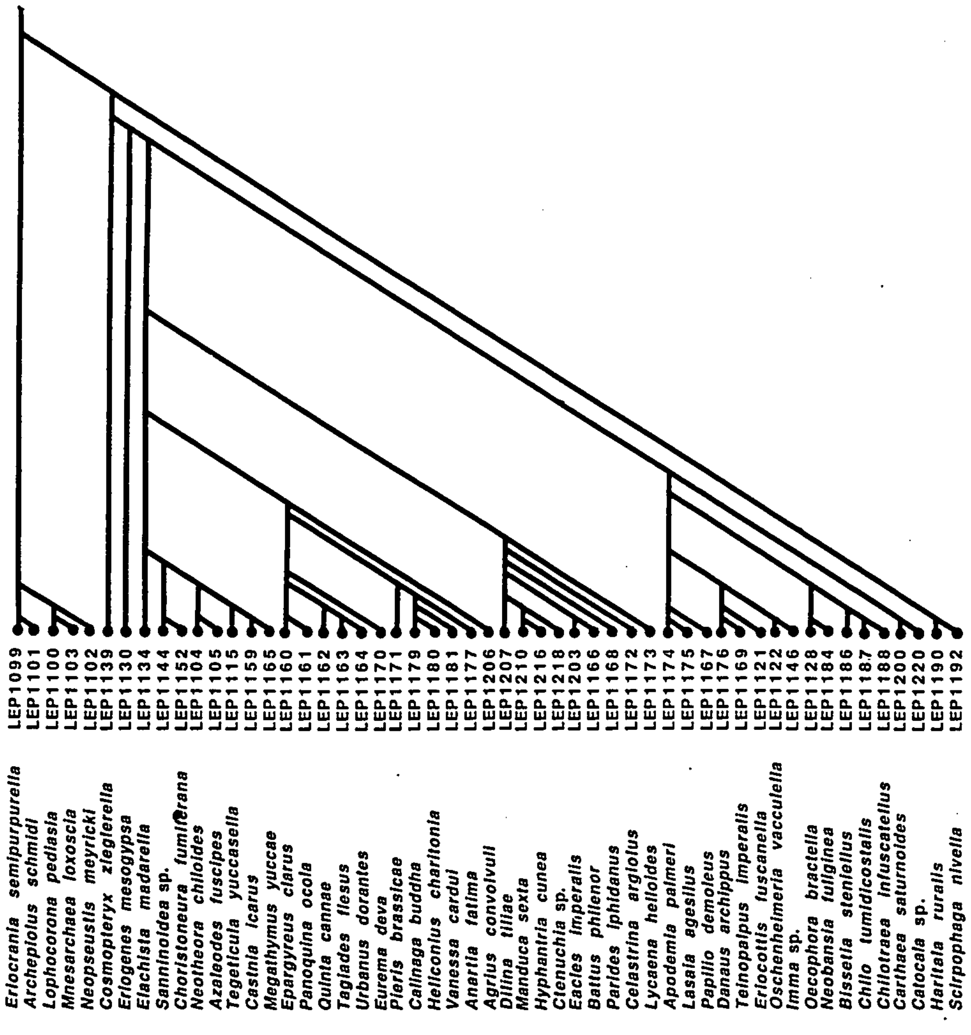

LEP1099 Eriocrania semipurpurella
LEP1101 Archepiolus schmidi
LEP1100 Lophocorona pediasia
LEP1103 Mnesarchaea loxoscia
LEP1102 Neopseustis meyricki
LEP1139 Cosmopteryx zieglerella
LEP1130 Eriogenes mesogypsa
LEP1134 Elachista madarella
LEP1144 Sanninoidea sp.
LEP1152 Choristoneura fumiferana
LEP1104 Neotheora chiloides
LEP1105 Azaleodes fuscipes
LEP1115 Tegeticula yuccasella
LEP1159 Castnia icarus
LEP1165 Megathymus yuccae
LEP1160 Epargyreus clarus
LEP1161 Panoquina ocola
LEP1162 Quinta cannae
LEP1163 Tagiades ilesus
LEP1164 Urbanus dorantes
LEP1170 Eurema deva
LEP1171 Pieris brassicae
LEP1179 Calinaga buddha
LEP1180 Heliconius charitonia
LEP1181 Vanessa cardui
LEP1177 Anartia fatima
LEP1206 Agrius convolvuli
LEP1207 Dilina tiliae
LEP1210 Manduca sexta
LEP1216 Hyphantria cunea
LEP1218 Ctenuchia sp.
LEP1203 Eacles imperalis
LEP1166 Battus philenor
LEP1168 Parides iphidanus
LEP1172 Celastrina argiolus
LEP1173 Lycaena helloides
LEP1174 Apodemia palmeri
LEP1175 Lasaia agesilus
LEP1167 Papilio demoleus
LEP1176 Danaus archippus
LEP1169 Teinopalpus imperalis
LEP1121 Eriocottis fuscanella
LEP1122 Oschenheimeria vacculella
LEP1146 Imma sp.
LEP1128 Oecophora bractella
LEP1184 Neobansia fuliginea
LEP1186 Bissetia steniellus
LEP1187 Chilo tumidicostalis
LEP1188 Chilotraea infuscatellus
LEP1200 Carthaea saturnoides
LEP1220 Catocala sp.
LEP1190 Haritala ruralis
LEP1192 Scirpophaga nivella
SIPHONATE MOUTHPARTS

FIGURE 84. Cluster analysis dendrogram of taxa comprising the Siphonate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

and maxillary palp development. They are united by the presence of long siphons, a condition that was documented anecdotally by Taylor (1957) and Willemstein (1987) and by prominent, squamate, three-segmented labial palps. The other four subclusters are topologically peripheral and are less diverse (two are monotaxic); they are differentiated by features of the antennae and mandibular, pharyngeal and labial regions. Eleven characters provide most of the separation for the seven subclusters. They are head shape, rostrum/proboscis development, frontal/vertical region development, antennal type, hypopharyx type, epipharynx type, mandible type, mandibular dentition, type of maxillary appendages, maxillary palp segmentation and aspect ratio, and labial palp type.

Subcluster 1 consists of three families (Eriocraniidae, Neopseustidae and Mnesarcheidae) of the suborder Dacnonympha (bracketed by data-set nos. 1099 to 1102 of Fig. 84). These forms possess short siphons and evident, often functioning, mandibles. Subclusters 2 (data-set no. 1139) and 3 (data set no. 1130) comprise respectively the families Cosmopterygidae and Stenomatidae of the superfamily Gelechioidea. These two clusters possess unique character-states for antennal type, hypopharynx type, epipharynx type and maxillary palp aspect-ratio. Subcluster 4 (1134 to 1206) comprises the most eclectic assemblage of any subcluster, with members from the suborders Exoporia, Monotrysia and Ditrysia and includes 12 families in nine superfamilies. Subcluster 5 (1207 to 1173) consists of advanced ditrysan taxa, principally butterflies and large, nectarivorous moths representing six families from four superfamilies. The third central subcluster, Subcluster 6 (1174 to 1220), consists of a broad spectrum of primitive to advanced ditrysan moths and butterflies, representing 11 families from seven superfamilies. Lastly, the extremely isolated Subcluster 7 contains two pyralid taxa (1190, 1192).

Geochronologic History. Understanding of the fossil history of siphonates has undergone dramatic revision during the last 20 years. Recent discoveries of exceptionally-preserved siphonate fossils in Jurassic sediments and Cretaceous ambers have altered the orthodox view of lepidopteran history from one discounting any pre-Tertiary lepidopteran ancestry (Ehrlich and Raven 1969) to one indicating that the Leipdoptera was present during the Early Jurassic and may be as old as the Triassic. It now appears that lepidopterans experienced a radiation of zeuglopteran groups during the Jurassic, followed by the origin of dacnonymphan, exoporian, monotrysan and primitive ditrysan forms during the Early Cretaceous. This was succeeded soon thereafter by the probable Late Cretaceous origin of the Papilionoidea (butterflies) (see Skalski 1979b, Wilson 1978a, Whalley 1986, Kozlov 1988). Similar changes in thinking have occurred among lepidopteran systematists, with recent discovery of various extant, primitive microlepidopteran groups in South America and the Southwest Pacific (Kristensen 1978, 1984b; Kristensen and Nielson 1983; Nielson 1978, 1985, 1987; Nielson and Scoble 1986), providing us with a richer account of the systematic relationships among extant primitive lepidopteran groups. Factors accounting for the considerable gap in our knowledge of lepidopteran systematics and fossil history have been (i) the poor preservational potential of siphonates as fossils and the relatively recent discovery of Cretaceous amber deposits and (ii) avoidance of capturing smaller, primitive, often taxonomically difficult Recent "microlepidoptera" in favor of the more systematically tractible "macrolepidpotera."

Several synapomorphies are shared between the Trichoptera and Lepidoptera (collectively, the Amphiesmenoptera), although most occur on the adult state (Razowski 1974, Hennig 1981) and virtually none on the wings (Kristenen, in Hennig 1981; Scott 1986). Recently it has been demonstated that the hindwings of both groups may be differentiated by the presence of scales in lepidopterans (Whalley 1986), a feature which can be preserved on fossil specimens. The earliest trichopteran is of Early Triassic age (see Section 8.5.2), indicating the lepidopterans must have had an ancestry, currently undocumented, to the Early Triassic. Although the earliest claimed lepidopteran is *Eoses triassica* Tindale, represented by a series of wings (Tindale 1945, 1980) from the Upper Triassic of Australia [79], this assignment has not been verified by other systematists, who maintain that *Eoses* is probably a mecopteran or an amphiesmenopteran (Riek 1955, Hennig 1981, Whalley 1986). The controversy is based principally on interpretations of a few connecting wing veins between some of the major longitudinal wing veins. Nevertheless, Tindale has described a second presumptive lepidopteran from the same deposit, *Eocorona iani* Tindale, which Whalley (1986) considers a possible lepidopteran, Shields (1988) a trichopteran and Skalski (1984b) either a mecopteran or a trichopteran. If Tindale's assignment is correct, then the current modified view of lepidopteran ancestry (Razowski 1974, Hennig 1981, Whalley 1986) needs to be seriously re-evaluated.

Currently, the oldest reliably documented lepidopteran is *Archaeolepis mane* Whalley from the Lower Jurassic of Dorset, England [69], whose identity was confirmed by the presence of undoubtable lepidopteran hindwing scales (Whalley 1985). In a recent discussion, Shields (1988) claims that terrestrial zeuglopteran lepidopterans arose from aquatic necrotaulid trichopterans between the Middle Triassic (*Eocorona*) and the Early Jurassic (*Archaeolepis*) and rapidly coevolved with primitive angiosperm hosts, basing his argument on biogeographical evidence of primitive lepidopteran taxa and their primitive host plant biology (see also Shields 1976). (See Fig. 85 for a phylogram and fossil occurrences of the siphonate mouthpart class.)

Although *Archaeolepis* is placed in a new monotypic family, the Archaeolepidae, probably because it consists only of a wing, it is impossible to align it with any modern primitive lepidopteran facies. A second, more complete, Jurassic microlepidopteran is *Eolepidopteryx jurassica* Rasnitsyn 1983 from the USSR [60] and, although it is placed in another monotypic family (Rasnitsyn 1983), it nevertheless has many features of extant mandibulate micropterygid moths (Shields 1988). From the Lower Cretaceous Baisa deposits of the USSR [52], nepticulid and lyonetid leaf-mines have been described on plesiomorphic angiospermous leaves (Skalski 1979b, Kozlov 1988). These mines indicate the presence of monotrysan and primitive ditrysan lineages during early angiosperm diversification.

Two primitive lepidopterans or amphiesmenopterans, of Late Jurassic and Early Cretaceous ages, have recently been accorded subordinal

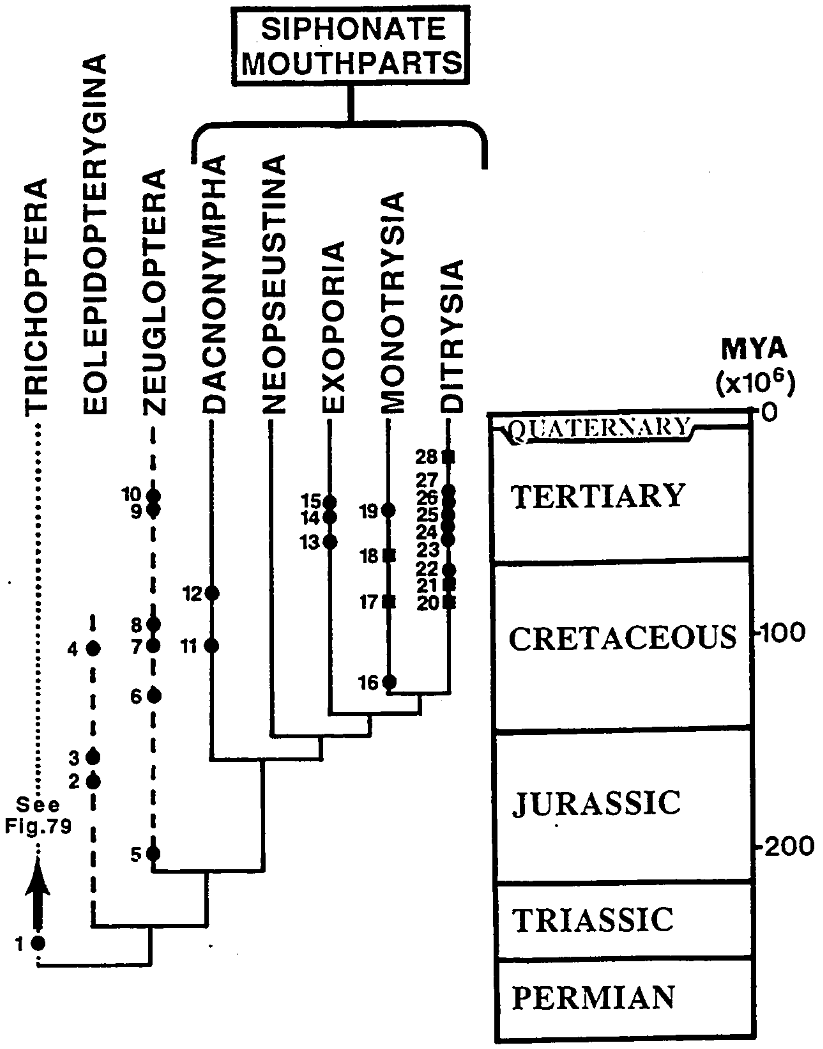


FIGURE 85. Geochronologic history of the Siphonate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Razowski (1974), Hennig (1981), Kristensen (1984a) and Kobayashi and Ando (1988). The level of taxonomic analysis is the suborder. The outgroup is Trichoptera. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

status and may represent a sister-group to the Lepidoptera (Kozlov 1988). Members of this group, the Eolepidopterygina, are *Eolepidopteryx jurassica* Rasnitsyn [60] (*vide supra*) and *Daiopteryx rasnitsyni* Skalski from the Lower Cretaceous of Baisa, USSR [52] (Rasnitsyn 1983, Skalski 1984a, Whalley 1986). These mothlike forms are mandibulate and contain reproductive structures unlike extant zeuglopterans (Whalley 1986).

From Cretaceous ambers and sediments many recently discovered specimens document the presence of several major siphonate lineages. Whalley (1978) documented from Lower Cretaceous amber of Lebanon [55] the micropterygid moth *Parasabatinca aftimacrai* Whalley. From this deposit an undescribed homoneuran moth is also known (Whalley 1977, Skalski 1979a), the earliest body fossil indication of a nonzeuglopteran lepidopteran, and possibly a siphonate. Another nonzeuglopteran taxon, *Undopteryx sukatshevae* Skalski, a lepidopteran of probable eriocranoid affinity from the Lower Cretaceous of Transbaikalia, USSR [52] (Skalski 1979a, Kozlov 1988), indicates the presence of the dacnynymphan lineage. From lowermost Upper Cretaceous amber of northwest France [45], Schlüter (1975, 1978) has documented micropterygid scales. However, of all Cretaceous amber deposits, the Upper Cretaceous Taimyr amber locality of Siberia [37] has proven the most productive (Zherikin and Sukacheva 1973, Skalski 1979b). From this deposit an unidentified caterpillar, a probable lophocoronid, and an incurvariid have been recovered (Skalski 1979b, Whalley 1986, Kozlov 1988). Finally, from the uppermost Cretaceous amber of Cedar Lake, Canada [35], a probable tineid larva and an undescribed heteroneuran adult (MacKay 1970, Skalski 1979a) has been documented. These discoveries of body fossils and leaf-mines provide direct and indirect evidence for the presence of zeuglopterans, dacnonymphans, exporians and monotrysans during the Early Cretaceous and the presence of ditrysans during the Late Cretaceous.

Indirect evidence from Late Cretaceous Turonian-Campanian floras indicate that synpetalous and syncarpous zingiberaceous flowers with united styles were present, contributing evidence for the presence of specialized pollinators, including siphonates and glossates (Friis 1985, Crepet and Friis 1987). Additionally, a coevolved association between the micropterygid moth *Sabatinca* and the primitive angiosperm *Zygogynum* (Winteraeae) from New Caledonia, both of which have Early Cretaceous representatives, indicates that the origin of pollination in siphonate ancestors may have began with the chewing of pollen on flower surfaces that were also used as mating stations (Thien et al. 1985).

Although direct evidence for siphonates with elongate siphons does not occur during the Cretaceous, the indirect evidence of Paleocene and Eocene flowers with funnelform and salverform corollas indicates a prior existence (Crepet 1979a,b, 1984; Crepet and Friis 1987). Furthermore, the Middle Eocene Green River Shale [23] documents the first appearance of papilionoid siphonates representing two families (Durden and Rose 1978). Later, during Early Oligocene times, the Florissant fauna [15] minimally contained four families of butterflies (Wilson 1978b). In the approximately coeval sediments of the Bembridge Marls of England [18], Jarzembowski (1980) described a diverse fauna of siphonates that included three families of butterflies. Ironically, Baltic amber [19] lacks any papilionoid siphonates, probably because of taphonomic biases, although it contains a diverse assortment of other siphonates (Skalski 1973a-c, 1974a,b, 1976a-c; Larsson 1978; Kozlov 1987). From the above discussion and a cautious acceptance of Wilson's (1978b) analysis of Paleogene insect faunas from western North America, one can conclude that of the four major holometabolan anthophilous mouthpart groups (adult-ectognathates, labellates, siphonates and glossates), siphonates and glossates have experienced the greatest percentage increase in familial diversity during the Paleogene.

Previous Designations. Mouthparts of insects that are herein termed siphonate have had a confusing nomenclatorial history. Fabricius (1775, 1799) considered lepidopterans as a type of insect with sucking mouthparts that he termed "Glossata." Clairville (1798-1806) and MacLeay (1821) placed trophic lepidopterans in their formal taxon, "Haustellata." Their "haustellate" nature was reaffirmed by Metcalf (1929) and James and Harwood (1969), who considered them siphoning haustellates and haustelates with lepidopteran mouthparts, respectively. Apparently the term haustellum signified any structure used for imbibing liquid food and not a stylet sheath. Ross et al. (1982) later focused on a functional attribute by classifying the lepidopteran siphon as "siphoning type" mouthparts. Recently, Chaudonneret (1986) discussed the structure of the lepidopteran proboscis, which he termed, "*la spiritrompe des palillions*." Notably, he included both haustoriate and siphonate mouthparts under a broader designation, "*pièces buccales lecheuses*," indicating a similarity based more on the form of the food imbibed rather than mouthpart structure or function. (See Table 6 for the history of nomenclature of siphonates.)

I am using the term **siphonate** to describe this mouth part class because it succinctly summarizes the structure of the principal food-procuring organ shared by all members of the class.

Review of Literature. For a mouthpart class as diverse and important as siphonates, surprising little has been written regarding mouthpart structure. This is probably attributable to the highly stereotyped mouthparts of siphonates, for which additional descriptions would provide little additional insight. Most formal mouthpart descriptions concern the conspicuous butterflies and larger moths, although the work of Kristensen (1968a,c; 1978) and Nielsen (1978, 1987) have reversed the trend by including descriptions of atypical mouthpart structures in several primitive, small moths. The seminal treatment of siphonate head and mouthpart structure is Eastham and Eassa (1955), who initially identified the structure and function of the siphon and provided an account of the frontoclypeal sucking pump. Other studies examining the musculation and function of the lepidopteran sucking pump include the taxonomically broad account of Schmitt (1938), Zaka-ur-Rab (1963) for the hypsid *Argina cribaria* Clerck and Fleming (1968) for several sphingid moths.

There are several studies of the head and mouthpart structure of siphonates. For primitive siphonates, Kristensen (1968a,b) provided a description of the eriocraniid *Eriocrania haworthi* Bradley, and Kristensen (1968c) and gave accounts of the mnesarchaeid *Mnesarchaea loxoscia*

Meyrick and the neopseustiid *Neopseustis meyricki* Hering. Vasudeva (1956) and Srivastava (1957) examined the palpilionid butterfly *Papilio demoleus* Linneaus, whereas Burgess (1880) and Kellogg (1893) had provided earlier accounts of the danaiid butterfly *Danaus archippus* (Fabricius). Later, Ehrlich (1958a) gave a more complete description, focusing on the musculature of *Danaus plexippus* Linneaus. Lastly, several studies of pyralid head and mouthpart structure included Pradhan and Aren (1941) for *Scirpophaga nivella*, Puri (1957) for *Chilo tumidocostalis* Hampson, and Rouchy (1964) for *Haritala ruralis* (Scopoli). More taxonomically comprehensive studies of head and mouthpart structure include Miller (1971) for the Hesperoidea and Castniidae, Ehrlich (1958b) and Ehrlich and Ehrlich (1962) for the Papilionoidea, and Puri (1958) for the Pyralidae.

Taxonomic descriptions, including monographs, were useful in obtaining head and mouthpart data on rare taxa or common taxa not described in the formal mouthpart literature. A partial listing of these monographs include the following descriptions of new monotypic taxa: Common (1973) for the lophocoronid *Lophocorona pediasia* Common, Mutuura (1971) for the neopseustid *Archepiolus schmidi* Mutuura, and Nielson (1987) for the palaeophatid *Azaleodes fuscipes* Nielsen. More derived, "microleoidopteran" taxa included the oschenheimeriid *Oschenheimeria vacculella* Roesslerstamm by Davis (1975), the oecophorid *Oecophora bractella* (Linneaus) by Clarke (1941), the stenomatid *Eriogenes mesogypsa* Meyrick by Duckworth (1973), the elachistid *Elachista madarella* (Clemens) by Braun (1948), and the tortricids *Tortrix loeflingiana* (Linneaus) and *T. viridana* Linneaus by Silvestri (1924).

Whalley (1971) has provided description of the thyridid *Neobansia fulginea* Whalley, and Michener (1952) has done likewise for the saturniid *Eacles imperialis* (Drury).

Lastly, several taxonomically eclectic studies of siphonate mouthpart elements have provided valuable comparative data. These include Shortt (1951) for head capsule endoskeletization and musculature, Breitenbach (1882), Taylor (1957) and Kristensen and Nielson (1881) for proboscis structure and musculation, and Walter (1885a) and Philpott (1927) for maxillae structure. Jordan (1923) and Philpott (1925) have described unusual structures on the head and labial palps of several siphonates.

8.6.3. Siphonomandibulate Class (Class 21)

Description. Head quadrate or vertically prolonged, nonretractile, with long proboscis. Genal region moderately to minimally developed; gula prominent and well-developed. Antennae variable; ocelli absent; compound eyes moderately developed, dichoptic. Mouthparts hypognathous (rarely prognathous).

Clypeus single, quadrate; labrum single, quadrate, margin variable. Hypopharynx and epipharynx variable. Mandibles dicondylic; falcate to tetragonal; dentition variable; musculated by adduction/abduction. Maxillae with elongated stipes, bearing galeae, laciniae and palps. Maxillary palpi 4-segmented, long. Galeae or maxillary palpi in most forms conjoined to form a siphon. Labium equant, with ligula (glossae) and palps. Labial palps 3-segmented, filliform to (rarely) tubular-siphonate. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. The distinctiveness of the Siphonomandibulate mouthpart class is the presence of an unique combination of character-states which individually occur in other mouthpart classes. Siphonomandibulates have joint possession of well-developed, trophic mandibles *and* a galeal or palpal siphon. Additionally, siphonomandibulates possess the singular combination of a long galeal or palpal proboscis plus typical coleopteran features such as absence of ocelli and paraglossae, four-segmented maxillary palpi and three-segmented labial palpi. Mouthpart classes that can be confused with siphonomandibulates include adult-ectognathate (Section 8.3.4) and siphonate (8.6.2), but neither of these classes have the combination of character-states mentioned above.

Diversity and Natural History. Within insects there were apparently several solutions to the imbibation of surface fluids by use of a siphon. Overwhelmingly the most taxonomically diverse clade that underwent this major transformation in mouthpart structure were adult lepidopterans, most of which comprise the Siphonate Class (see Section 8.6.2). The remaining examples of siphonate-style mouthparts occur among coleopterans and include at least three clades that have independently originated siphonate mouthparts designed for the suction of surface fluids, principally nectar (Fig. 86). Five genera belonging to three families occur among these three siphonomandibulate clades, namely the rhipiphorid genera *Macrosiagon* and *Rhipiphorus*, the nemognathine

INCLUDED TAXA:
Coleoptera (Meloidae, Rhipiphoridae)

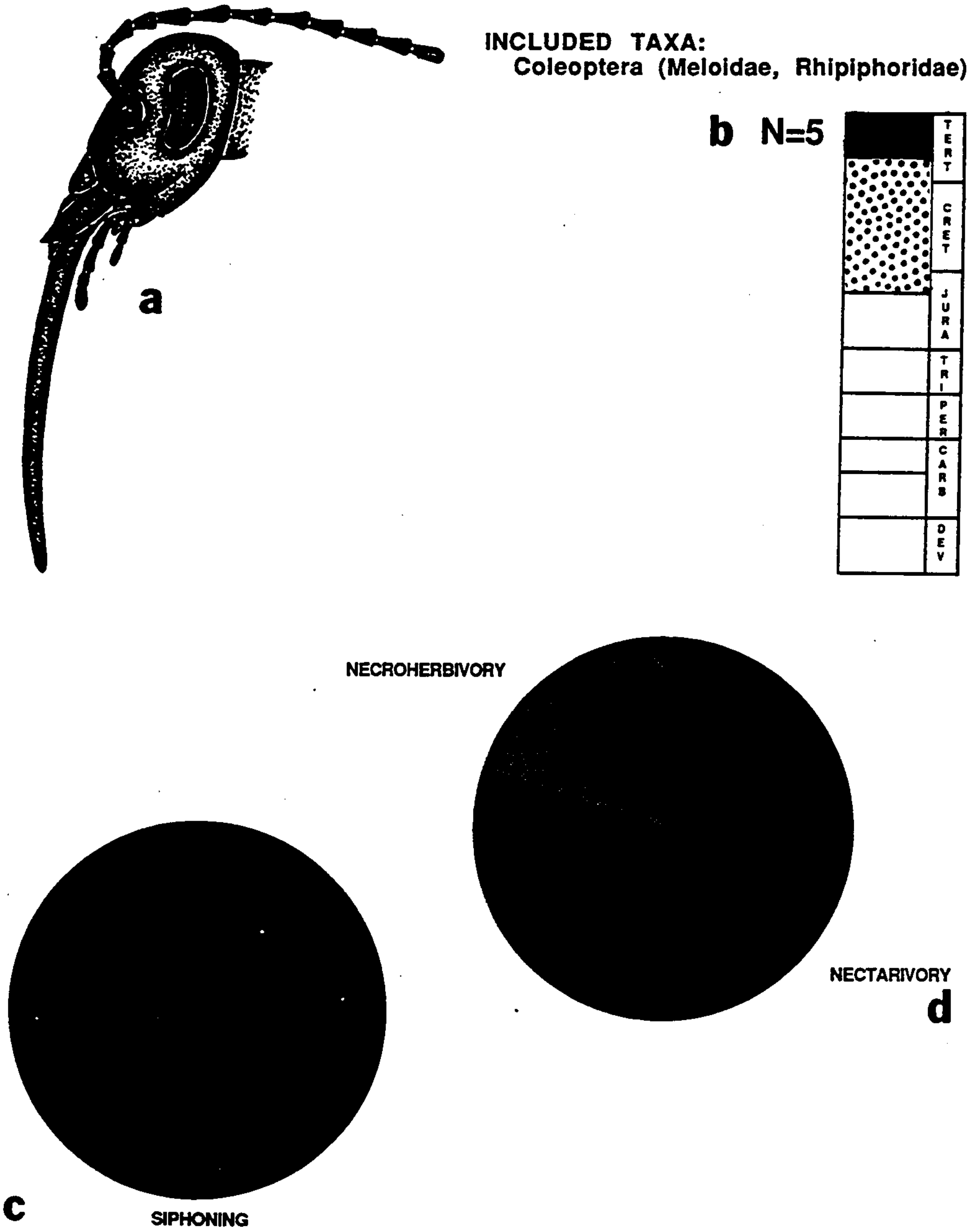


FIGURE 86. Overview of the Siphonomandibulate Mouthpart Class. a, *Nemognatha piezata* Fabricius (Coleoptera: Meloidae, data-set no. 679); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-group; d, dietary spectrum.

meloid genera *Nemognatha* and *Leptopalpus* and the sphaeridiine hydrophilid, *Aculomicrus*. These five, mostly flower-frequenting genera are estimated to have a species diversity of about 450 (Appendix D) and thus represent a rank-order of 32 out of 34 mouthpart classes (Table 5, Fig. 131). This absence of ecological importance is probably attributable to competition from other nectarivorous mouthpart classes such as siphonates, glossates and perhaps adult-ectognathates. However siphonomandibulates are a poorly understood group and most of the ecological documentation for this group is for a few common species of *Nemognatha*; *Aculomicrus* was only recently described by Smetana in 1975.

The proboscis of *Nemognatha* can extend to 1.2cm (Proctor and Yeo 1973), reaching the length of its body (Faegri and van der Pijl 1980). The proboscal length of *Leptopalpus* is similarly long and extends to its hind tarsi (Handschin 1929). These and other siphonomandibulate proboscides are unusual when compared to the typical coleopteran "mess-and-soil" pollination syndrome, wherein pollen and nectar are consumed by the use of prominent, slashing mandibles and typical generalized maxillae and labia (Faegri and van der Pijl 1980). Nevertheless, galeal elongation among anthophilous forms is relatively common (Fuchs 1974, Grinfel'd 1975) and is associated with sequestering pollen or nectar by setal entrapment or capillary adsorption, respectively. Thus it seems likely the the coleopteran siphon originated from elongate galeae already used for nectarivory by sponging. Although there has been minimal study of the mechanism of fluid uptake for siphonomandibulates, Smith (1898), Packard (1898) and Crowson (1981) have indicated that the elongate galeae in *Nemognatha* are tubular in cross-section, a conclusion that was previously doubted by Grinfel'd (1975). Fuchs (1974) documented the presence of outer spatulate setae on the proboscis of *Nemognatha*, structures which presumably could sequester fluid food. It has been well established that *Nemognatha* is a nectarivore (Kugler 1979, Arnett and Jacques 1981, Faegri and van der Pijl 1980). *Leptopalpus* bears a siphon constructed from conjoined maxillary palps that are densely setate on their mesial surface (Handschin 1929). The situation for the siphons of *Macrosiagon* and *Rhipiphorus* is probably similar, although Rivnay (1929) did not discuss galeal specializations in his extensive taxonomic account of North American rhipiphorids.

Smetana (1975) described the unique mouthparts of *Aculomicrus pusio* Smetana, in which an elongate, bifid ligula and elongate, labial palps with setation on their mesial surface collectively form a tubular labial funnel for siphoning liquid food. The diet of this small semi-terrestrial hydrophilid includes rotting fruit and decomposing litter (Smetana 1975). The construction of the siphon of *A. pusio* is different than the galeal siphon of lepidopterans, nemognathine meloids and the palpal siphon of rhipiphorids, and thus constitutes a third, distinct way of co-opting various mouthpart elements to form a suctorial siphon.

Structural Themes. Two major subclusters, each with a structural theme, are recognized in Fig. 87. The first theme consists of a subcluster of four tenebrionoid (=heteromeran) taxa consisting of rhipiphorids and meloids (entries 653, 655, 677, 679); the second theme is the structurally unique subcluster of the single hydrophilid taxon, *Aculomicrus pusio* Smetana (entry 480). The first subcluster is

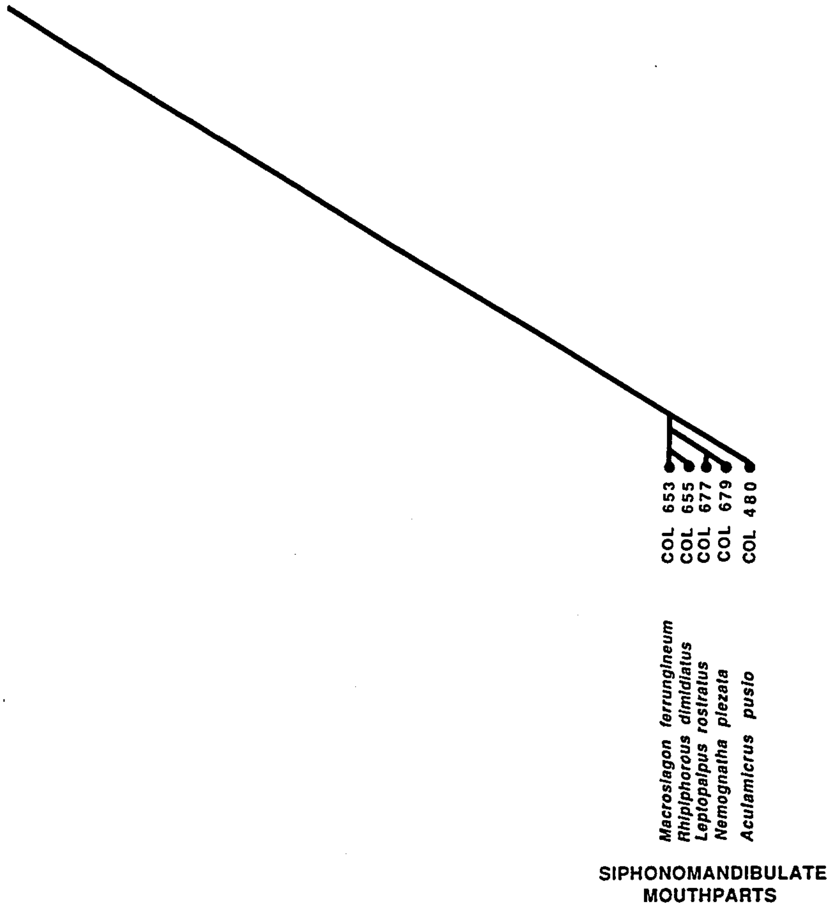

COL 653 Macrosiagon ferrungineum
COL 655 Rhipiphorous dimidiatus
COL 677 Leptopalpus rostratus
COL 679 Nemognatha piezata
COL 480 Aculamicrus pusio
SIPHONOMANDIBULATE MOUTHPARTS

FIGURE 87. Cluster analysis dendrogram of taxa comprising the Siphonomandibulate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

characterized by the presence of trophic siphons consisting of maxillary elements of either conjoined galeae or conjoined maxillary palps. The second subcluster consists of a taxon in which labial elements participate in the formation of a trophic siphon. These subcluster-based differences however are not as significant when compared to to subclustering patterns in more taxonomically diverse mouthpart classes (cf. Fig. 36).

Geochronologic History. Little is known about the geochronologic history of the Siphonomandibulate Mouthpart Class. Three major reasons currently mitigate against a better understanding of the timing of origin of colepteran siphons in these three diverse clades: (i), there is a poor fossil record of most terrestrial anthophilous beetles; (ii), the level of analysis is at the genus and not the family or higher, making taxonomic resolution difficult; and (iii), if there are fossil genera other than those that currently are known to have siphonomandibulate mouthparts, they would be difficult to detect in most nonamber Mesozoic or even Cenozoic deposits. Fig. 88 presents an inferred geochronologic history of siphonomandibulates, using cladistic relationships of extant groups and their scant fossil records. There is a modicum of evidence indicating a Late Jurassic or Cretaceous origin form siphonomandibulate clades.

Previous Designations. The term siphonomandibulate, to my knowledge, has no prior usage in the entomological literature. As a name for a mouthpart class **siphonomandibulate** refers to the joint presence of mouthpart elements capable of chewing (mandibles) and other elements for

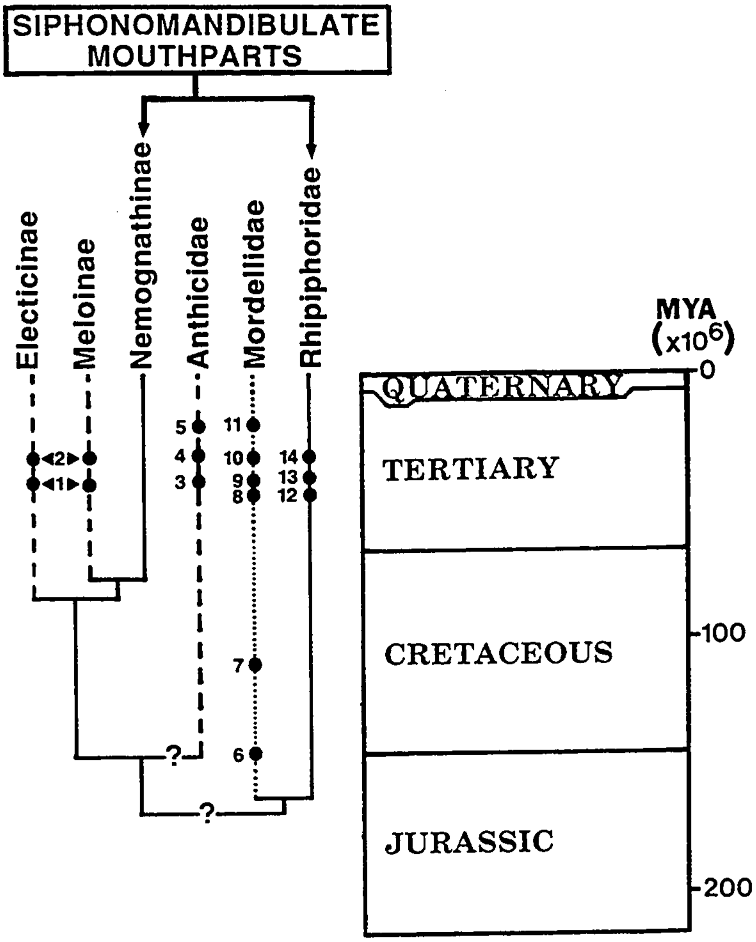


FIGURE 88. Geochronologic history of the Siphonomandibulate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Crowson (1976, 1981). The taxonomic level of analysis is the family and subfamily. The outgroup is Mordellidae. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

siphoning fluid food (a maxillary or labial siphon). Thus the designation appropriately renders the two most diagnostic features defining members of this mouthpart class. (See Table 6 for a history of nomenclature.)

Review of Literature. The galeal proboscis of *Nemognatha* has attracted the attention of morphologists for over a century. Galeae of *Nemognatha* were figured by Hagen (1881), Smith (1898), Packard (1898), Crampton (1923b) and Williams (1938) among others, and comment has been provided by Grinfel'd (1975) in the context of the origin of beetle pollination of angiosperms and by Crowson (1981) who mentioned the nemognathine proboscis as a unique adaptation for nectarivory by beetles. Both Stickney (1923) and Grinfel'd (1975) have figured the head and associated mouthparts of *Nemognatha*. Handschin (1929) presented a structural description and functional analysis of the palpal siphon of *Leptopalpus*, an interpretation that was reiterated by Grinfel'd (1975). The rhipiphorids *Macrosiagon* and *Rhipiphorus* have been variously described by Stickney (1923), Rivnay (1929), Williams (1938) and Grandi (1959), although none of these authors adequately documented mouthpart structure to the degree that has been provided for *Nemognatha*. Fuchs (1974) has presented a stimulating discussion of mouthpart adaptation for pollinivory and nectarivory in beetles and mentions *Nemognatha* in passing.

8.7. Glossate Series

8.7.1. General Features of the Glossate Series

Since the membership of the Glossate Series consists of only one mouthpart class, glossates, the reader is referred to the subsequent discussion for details such as structure, natural history, diversity and geochronologic range.

8.7.2. Glossate Class
(Class 21)

Description. Head symmetrical, quadrate and proboscate; genal region dimunitive, gula present. Eyes obvious, lateral, oval to reniform; ocelli three. Antennae prominent and geniculate. Food pump cibarial. Mouthparts hypognathous and protractile; dominated by a maxillolabiate complex, with a prominent glossa of variable length.

Clypeus single, quadrate to transversely elongate; labium single, mostly vertically elongate. Hypopharynx inconspicuous, usually lobe-like; epipharynx fleshy. Mandibles dicondylic; falcate or excavate; incisiform and with a basal brush, or more commonly edentate; musculation characterized by adduction/abduction. Maxilla complete, fused by membrane to labium, bearing two basal sclerites and usually elongate stipes with a lever-based protraction/ retraction mechanism. Galeae amplexiform, tubular when appressed to labial region; lacinia variously developed. Maxillary palps small, often aciculate or setate. Labium bearing a glossa, paraglossae and palps. Single medial glossa fleshy, ranging from short (rarely bifid) "tongue" to long, flabellate, transversely-ridged, fleshy "tongue" with distal hairs. Paraglossae shorter;

commonly prominent and fleshy. Labial palps with 4 or more segments; very long and (often) forming a tubular passage with galeae for squeezing of fluid during glossal retraction. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. The glossate condition is polyphyletic within insects, reaching its greatest development in apoid hymenopterans (bees). Key features of glossates are (i) presence of a variously long, but prominent, single median glossa used for lapping fluid food (invariably nectar), (ii) long, labial palps with supernumerary segments, and (iii) a protrusible, elongate, maxillolabial complex that can be deployed into deep cavities for sequestering fluid food. This complex has long, rodlike cardines and stipites at its base that are surrounded by an extensible throat membrane. Although maxillolabiates (Section 8.3.6) possess a maxillolabial complex, it is not designed as a protractile, elongate organ for lapping fluid food; their glossae is diminutive by comparison to glossates. Also, maxillolabiate mandibles are never excavate and used for molding mud or liquified paper for nest construction, but are falcate and used for cutting and shearing animal or plant tissue.

Diversity and Natural History. Glossates constitute the most important animal pollinator of angiosperms (Armstrong 1979, Crepet and Friis 1987, Bertin 1989). Nevertheless they only comprise three percent of all hexapod species and in terms of diversity, glossates represent 15 families, 850 genera and approximately 27,000 species (Appendix D), corresponding to a rank-order of 12 out of 34 mouthpart classes (Table

5, Fig. 131). Although glossates are a moderately diverse mouthpart class, their ecological role as angiosperm pollinators imparts an inordinate conspicuousness in many ecosystems. Together with siphonates and some labellates, glossates are the dominant faithful pollinators in recent ecosystems and imbibe not only nectar with their mouthparts, but also secure with chewing mandibles or with body hairs and various hair-formed "baskets," pollen, often as food for larvae (Fig. 89).

Within glossates, the dominant clade, Apoidea (bees), are most diverse in warm-temperate, xeric regions, especially Mediterranean-type climates and in some moist tropics, such as South America (Michener 1979). Bees are poorly represented in equatorial savannas, in arid, tropical regions and in some moist tropics (e.g. Africa). Wasps by contrast are unimportant at higher latitudes and are significant pollinators in the tropics (Kevan and Baker 1983). There apparently is no correlation between bee diversity and angiosperm diversity within a given area (Michener 1979), nor is there a correlation between primitive bees and pollination of primitive angiosperms (Bernhardt and Thien 1987). All glossates, including several groups belonging to the nonapoid aculeate Hymenoptera, or "flower wasps" (Sapygidae, Scoliidae, Vespoidea, Sphecidae), apoids (eight families of bees) as well as certain nemopteran planipennians, imbibe nectar. Many also imbibe plant secreted oils or are pollen collectors and/or consumers. Glossates, among all mouthpart classes, are heavily represented by subsocial and eusocial clades, including vespids, a few eumenids, and halictid, anthophorid and apid bees (Wilson 1971). Sociality apparently evolved independently at least 12 times (Wilson 1971, Winston and Michener 1977,

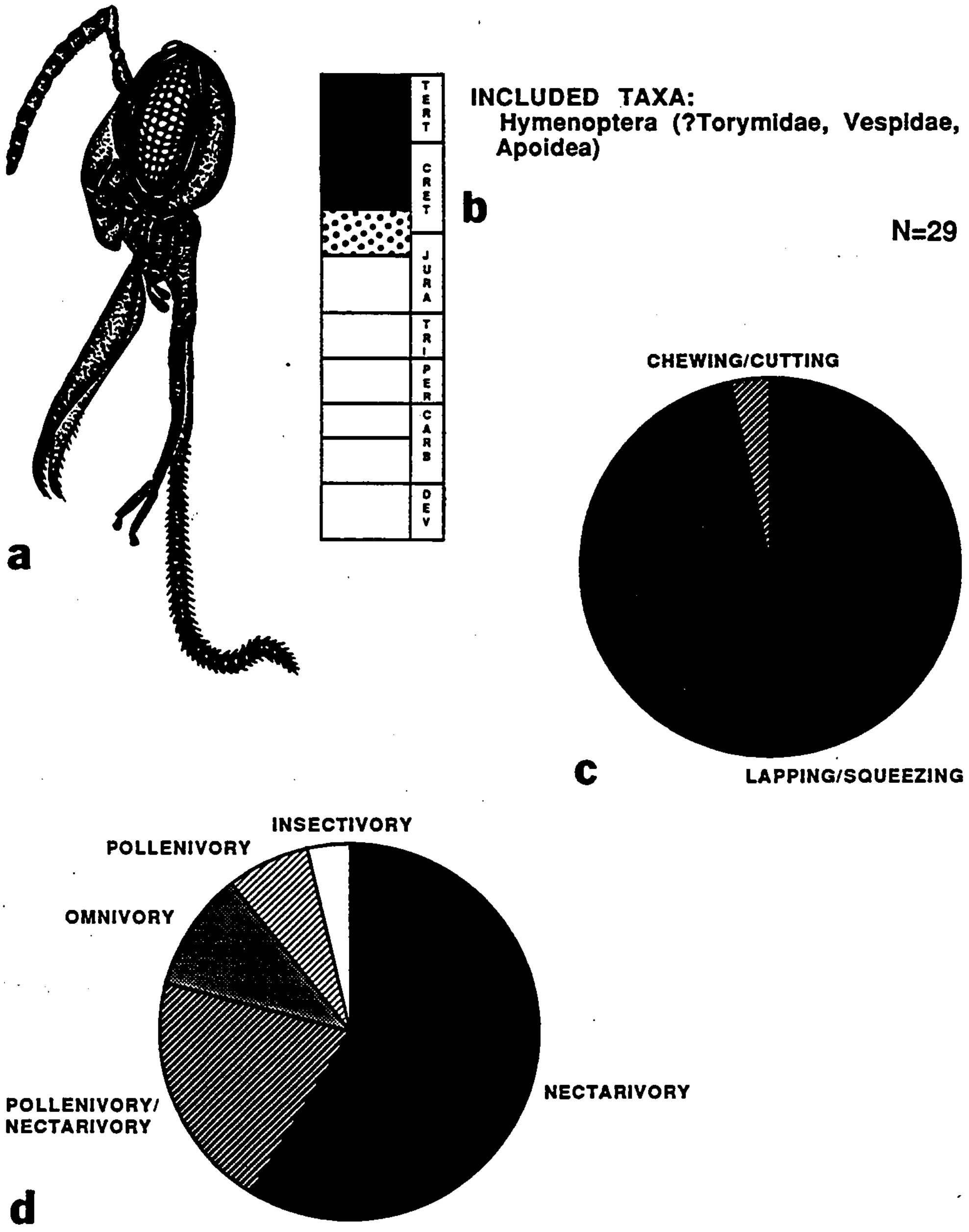


FIGURE 89. Overview of the Glossate Mouthpart Class. a, *Anthophora* sp. (Hymenoptera: Anthophoridae, data-set no. 1354), after Demoll (1908) and Michener (1944); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups, d, dietary spectrum.

Webster and Peng 1988). In most of these clades solitary forms are primitive pollinators and social forms are more derived pollinators.

Wasps that pollinate flowers have relatively short mouthparts, with projecting glossae that ranges from 1 to 3 mm., although some higher wasps have glossae 5 to 10mm long (Faegri and van der Pijl 1980). Chrysidids (cuckoo wasps) frequently have long proboscides (Kevan and Baker 1984). Anthiphilous wasps visit flowers frequently, preferring open bowl-shaped or short tubular flowers (Spradbury 1973, Kevan and Baker 1983). Although scoliids, sapygids, vespoids and sphecids are all known to imbibe nectar, only a few use nectar as a larval food; most anthophilous wasps continue the phylogenetically primitive behavior of provisioning larvae with macerated insect and arachnid corpses (Willemstein 1987). Nevertheless, a "wasp flower syndrome" has been established for several groups of highly anthophilous wasps. Wasp-pollinated flowers are of dull brown to ocassionally dull pink color consisting of horizontal or nodding cups into which a wasp can thrust its head (Müller 1883, Proctor and Yeo 1973, Kevan and Baker 1983). However this pollination syndrome is not well-constrained structurally according to Faegri and van der Pijl (1980) and some flowers such as those that mimic wasps and induce pollination through pseudocopulation (Proctor and Yeo 1973) are atypical of "wasp flowers." Nemopterids (spoon-wing lacewings) have convergent glossate mouthparts with many anthophilous wasps and though they are documented pollinivores (Picker 1987) they are probably also nectarivores.

Bees are far more important as agents of pollination than wasps; they are the dominant angiosperm nectarivores, favoring flowers with differentiated perianth whorls and the presence of filamentous stamens (see Waddington [1987] for bee nutrition). Their importance extends to the ubiquitous presence of a stereotyped floral design, the bee pollination syndrome, occurring in plant families as taxonomically dis parate as the Fabaceae, Lamiaceae, Violaceae, Scrophulariaceae, Orchidaceae and Ranunculaceae. The bee pollination syndrome consists of bilaterally-symmetrical, semienclosed and intricate flowers with hidden rewards of nectar, pollen or oil, great depth effect, bright color (mostly yellow or blue) with ultraviolet corollar guidemarks, strong but not overpowering odor, and concealed sexual organs with few stamens (Faegri and van der Pijl 1980; Kevan and Baker 1983). Bees apparently posses high flower-constancy and, unlike wasps, are capable of selecting flower species for pollination, even if they are rare (Barth 1985). For example, euglossine bees are remarkably efficient long-distance pollinators of tropical plants with extremely patchy or dispersed distributions and are capable of travelling up to 23km from a home nest for pollination of the same species (Janzen 1971). This behavioral feature has promoted angiosperm diversification by the selection of angiosperm speciation-promoting characteristics by (Crepet 1985).

There is a greater range of tongue length in bees than in wasps, with plesiomorphic bees possessing shorter, even bifid glossae, whereas apomorphic groups such as euglossine bees, have long glossae up to 30mm long (Barth 1985), rivaling that of many siphonates. These glossal structural differences are strongly associated with floral structural features, particularly corolla depth, of the pollinated flower: larger-tongued bees are able to pollinate deeper, often tubular flowers with deep-seated nectaries that produce nectar rich in sucrose sugar, whereas short-tongued bees pollinate bowl-shaped or short tubular flowers with nectar rich in hexose sugar (Kevan 1984, Martin 1986). Another associated trait is flower color. Purple Israeli crucifers are pollinated by long-tongued bees and white or yellow species are pollinated by short-tongued bees (Dukas and Schmida 1989). It would be of interest to determine whether these features--flower depth, nectar sugar type, flower color, or others--are strongly associated with each other (see Willemstein 1987). This ecological differentiation of short- and long-tongued bees is often bypassed by the phenomenon of nectar thievery, wherein wasps or bees with mandibles capable of tearing petal tissue construct holes at the base of corollas to rob the flower of nectar, without the benefit to the plant of pollination (Martin 1986).

A few studies provide some tentative insights into the role that glossates play in community-level ecology. Yumoto (1986) demonstrated that two major pollinators occur on alpine meadow plants in Honshu: (i) densely clustered plants pollinated by syrphid flies that are regionally distributed and undergo simultaneous blooming and (ii) bumblebee-type plants that are locally distributed in dispersed stands with staggered blooming phenologies. In the different ecological setting of a cool-temperate, mixed conifer-broadleaved forest, Yumoto (1988) found that bumblebees consistently favored the bell- or funnel-shapes of understory flowers over tubular canopy flowers. Pike (1978) discovered that bumblebees characteristically proceed up the axis of a vertically-oriented inflorescense when browsing, but when shifting to another infloresence, they start at the level that they left off from the previous inflorescense where nectar abundance is not the greatest. These and other highly stereotyped foraging patterns could have significant coevolutionary responses among the foraged plant species.

Structural Themes. Glossate mouthparts are characterized by five, major structural groups (Fig. 90). These groups are represented by the subclusters (i) *Ceratosolen acutatus*, a torymid fig wasp, (ii) the only nonhymenopteran, *Palmipenna aeoloptera*, a spoon-wing lacewing of the Order Planipennia, (iii) the sapygid *Fedtschenkia grossa* and the scoliid *Scolia bidens*, (iv) the vespid wasps *Vespa vulgaris* and *Vespula germanica* and (v) the largest subcluster, comprising all seven families of bees, the masarid wasp *Paragia odyneroides* and four sphecid wasps.

Although it is unclear whether the glossate condition in *Palmipenna* is shared by closely-related adult nemopterids, other nemopterids apparently have anthophilous habits (Arnett 1985). The occurrence of a small-sized, torymid wasp with glossate mouthparts as Subcluster 2 is unexpected and is probably related to convergent mouthpart specializations for pollinating very small florets of fig (*Ficus*) compound fruits. The group comprising sapygid and scoliid wasps also probably includes related families, such as Mutillidae and Tiphiidae, but since adults of these families were not included in the analysis, the limits of this subcluster remains unknown. The vespoids of Subcluster 4 consist of the families Masaridae, Eumenidae and Vespidae and comprise a well-defined subcluster characterized by possession of strong falcate mandibles, unlike the excavate mandibles of bees. Subcluster 5 comprises sphecid wasps and bees; inclusion of sphecid wasps should not be that surprising

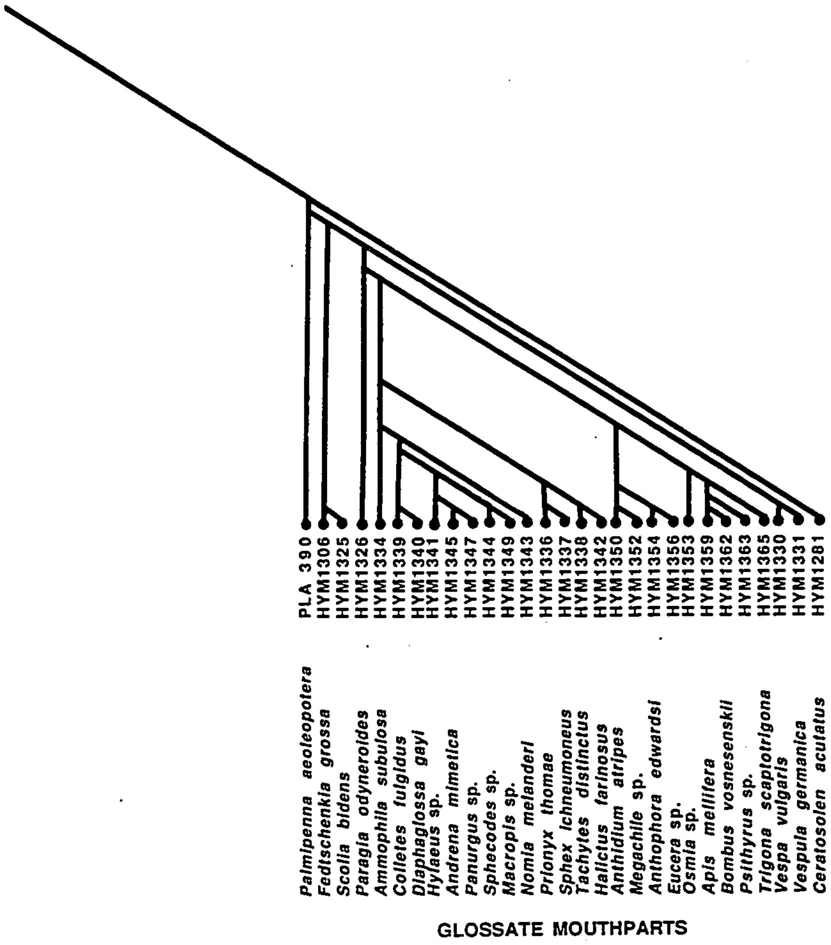

PLA 390 Palmipenna aeoleopotera
HYM1306 Fedtschenkia grossa
HYM1325 Scolia bidens
HYM1326 Paragia odyneroides
HYM1334 Ammophila subulosa
HYM1339 Colletes fulgidus
HYM1340 Diaphaglossa gayi
HYM1341 Hylaeus sp.
HYM1345 Andrena mimetica
HYM1347 Panurgus sp.
HYM1344 Sphecodes sp.
HYM1349 Macropis sp.
HYM1343 Nomia melanderi
HYM1336 Prionyx thomae
HYM1337 Sphex ichneumoneus
HYM1338 Tachytes distinctus
HYM1342 Halictus farinosus
HYM1350 Anthidium atripes
HYM1352 Megachile sp.
HYM1354 Anthophora edwardsi
HYM1356 Eucera sp.
HYM1353 Osmia sp.
HYM1359 Apis mellifera
HYM1362 Bombus vosnesenskii
HYM1363 Psithyrus sp.
HYM1365 Trigona scaptotrigona
HYM1330 Vespa vulgaris
HYM1331 Vespula germanica
HYM1281 Ceratosolen acutatus
GLOSSATE MOUTHPARTS

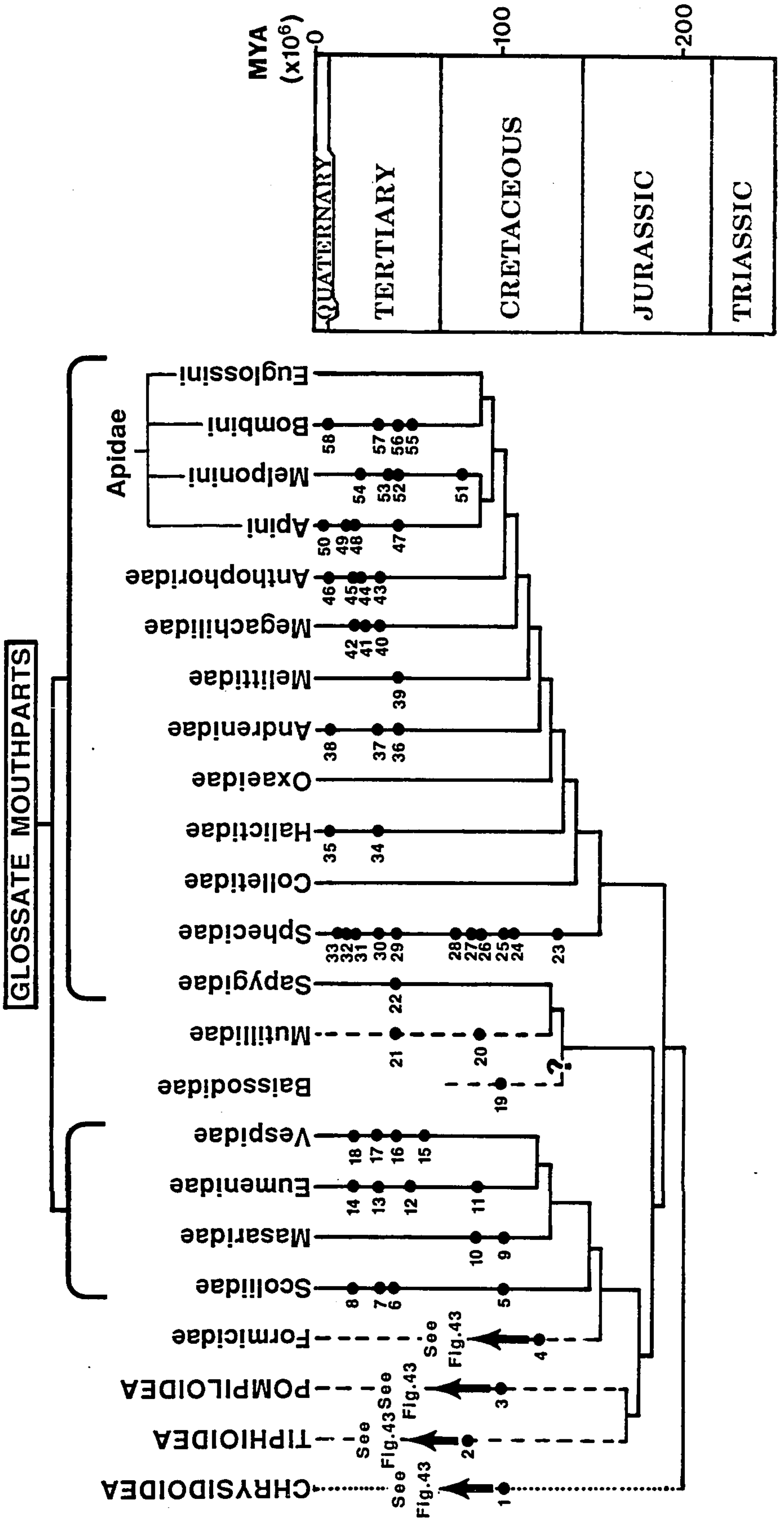
FIGURE 90. Cluster analysis dendrogram of taxa comprising the Glossate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

since sphecid wasps are very similar structurally to bees (Crepet and Friis 1987) and share mouthpart similarities to short-tongued bees.

Geochronologic History. The fossil record and current knowledge about the relationships of glossate insects indicates an origin of the mouthpart class among taxonomically disparate groups during the Late Jurassic to Early Cretaceous. The glossate condition as defined by the dendrogram of Fig. 90 originated at least five times: in certain nemopterid planipennians and in four monophyletic hymenopteran groups, the Torymidae, Sapygidae, Scoliidae-Vespoidea and spectacularly in the Sphecidae-Apoidea (Fig. 91). Virtually no fossil evidence can constrain the origin of the apparently modified glossate mouthparts of *Palmipenna*. The oldest nemopterid is from the Oligocene of Colorado [15], and although the head is rostrate, it is abbreviated and its mouthparts remain unknown. The sister-group of the Nemopteridae is probably the Ithonidae (Withycombe 1922), allowing minimally for an Early Tertiary origin for the Nemopteridae.

Sapygid wasps are known from Baltic Amber [19], although their sister-group, the Mutillidae, places the origin of sapygids during the Late Cretaceous because of the occurrence of the probable mutillid *Cretavus sibiricus* Sharov 1957 in Turonian strata [39] (Wootton 1986). (Mutillids are nectarivorous and may be glossates, but were not analyzed in this study.) Although tiphiids are the sister-group to the Mutillidae + Sapygidae and may also be glossate (again, no adults were analyzed), the occurrence of only Late Cretaceous Coniacian/Santonian tiphiid fossils [37] leaves the origin of the monophyletic clade of

FIGURE 91. Geochronologic history of the Glossate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Wilson (1971), Winston and Michener (1977) and Köningsmann (1978b). The level of taxonomic analysis is the family and the tribe within the Apidae. The outgroup is Chrysidoidea. For geochronology of the Nemopteridae, see Fig. 52. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.


MYA
(x10⁶)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
GLOSSATE MOUTHPARTS
Apidae
Euglossini
Bombini
Melponini
Apini
Anthophoridae
Megachilidae
Melittidae
Andrenidae
Oxaeidae
Halictidae
Colletidae
Sphecidae
Sapygidae
Mutillidae
Baissodidae
Vespidae
Eumenidae
Masaridae
Scoliidae
Formicidae
POMPILOIDEA
TIPHIOIDEA
CHRYSIDOIDEA
See Fig.43
See Fig.43
See Fig.43
See Fig.43
?

Tiphiidae + (Sapygidae + Mutillidae) within the Late Cretaceous, possibly earlier. By contrast the monophyletic glossate clade of Scoliidae + (Masaridae + [Eumenidae + Vespidae]) (Willemstein 1987) apparently arose during the Late Cretaceous based on the occurrence of the masarid *Curiovespa curiosa* Rasnitsyn 1975 [39] and the absence of scoliids earlier than the Tertiary. Both the Eumenidae and Vespidae are well-represented during the Tertiary and include recent genera.

The spectacular radiation of bees, as indicated by Early and Middle Tertiary deposits has often been a mystery in lieu of any known Cretaceous bee. However the recent celebrated discovery of the highly derived *Trigona prisca* Michener and Grimaldi 1988a in Campanian age New Jersey amber [36] has simultaneously answered the issue of the presence of mid-Cretaceous bees, but also called into question the timing of origin of all apoids. The presence of a markedly apomorphic melponine apid bee in the Late Cretaceous indicates that all other bee families had a prior, as yet unreported, existence. Furthermore biogeographical analyses of current bee distribution, including the very poor dispersal abilities of melponine bees was noted by Michener in 1979, who claimed that the most derived subfamilies of the most derived family of bees (Apidae) had a Gondwanan origin no later than mid Late Cretaceous for its constituent subgenera. This conclusion was supported by cladistic analyses and vicariant distributional patterns for other primitive bee groups, which indicated origin of the Apoidea from a sphecid wasp, possibly from the arid interior of West Gondwanaland (Michener 1979, Crepet and Friis 1987).

Sphecid wasps occur in several Early Cretaceous deposits, including the Weald Clay of England [57] (Jarzembowski 1984), the Koonwarra Bed of Victoria, Australia [53] (Jell and Duncan 1986) and from the Baisinsk Stratum of Baisa [52] (Rasnitsyn 1975); sphecids are also recorded from Late Cretaceous ambers from France [45] (Schlüter 1978), Siberia, USSR [37] (Evans 1973) and Manitoba [35] (Evans 1969). The combined evidence of the most derived ingroup occurring in Campanian deposits, a generalized, earliest outgroup ancestor occurring during Early Cretaceous deposits and knowledge about biogeographical patterns of primitive bee taxa, all point to either rapid, punctuational evolution of apoid glossates during the late Early Cretaceous, or evolution under a more gradual mode during the Late Jurassic. Occurrences of apoid glossates in Early Tertiary deposits (Kelner-Pillault 1969, 1970a; Zeuner and Manning 1976) suggest prior derivation of all major apoid families (though colletids, oxyaeids and euglossine apids lack fossils), including many derived lineages (Kerr and Cunha 1976; Burnham 1978; Willemstein 1980, 1987; but see Kelner-Pillault 1974).

Because of the importance of glossate mouthparts in the early diversification of angiosperms, two additional methods in addition to the examination of body fossils, have been used to infer the presence of the bee pollination syndrome during the Cretaceous. These are cladistic analyses of bee pollinators and their pollinated plants and evaluation of floral modifications from Cretaceous floras. Based on a study of the taxonomic relationships of primitive angiosperms and their pollinators, Bernhardt and Thien (1987) concluded that bee pollination in primitive angiosperms is polyphyletic. In fact the very derived genera *Trigona* and *Melipona* pollinate primitive angiosperm species in the tropics. The alternative approach, examination of floral structure in the fossil plant record, has yielded interesting data. The existence of the bee pollination syndrome is inferred from characteristic, preservable floral specializations from several floras of various types of preservational style (Friis 1985, Crepet and Friis 1987). From the Late Cretaceous floral record Crepet (1985) concluded that Late Cretaceous flowers indicate glossate pollination, and specifically by Turonian/Campanian times fossil flowers exhibit intrafloral fusion of the same elements, including syncarpy (but with superior ovaries), synpetaly and formation of a common style, consistent with a bee pollination syndrome. By the Middle Eocene [25] there are synpetalous funnelform flowers with wide corollas (Gentianaceae), zygomorphic zingerberaceous flowers and New World-type malpighiaceous flowers with sepals bearing characteristic oil glands virtually identical to extant species that are pollinated intensively by oil-collecting anthophorid bees. These fossils indicate the presence of three early pathways within the bee pollination syndrome. Also present during the Paleocene and Middle Eocene are woods and flowers from two of the most derived euphorbiaceous tribes (Crepet and Daghlian 1981) that also indicate bee pollination.

The more ultimate origins of primary nectarivory and secondary pollinivory among apoid glossates has been attributed to the development of an ancestral insectivorous wasp lineage that substituted pollen for insects as a partial source of dietary protein, followed by nectar utilization for feeding of dependent larvae (Grinfel'd 1973). Crepet (1979) envisions the origin of nectarivorous habits from such a lineage by the foraging of an insectivorous/pollinivorous wasp on Jurassic cycadeoids or Early Cretaceous angiosperms that bear a close juxtaposition of pollen-bearing organs and nectaries. By the time apoids evolved, the primitive insectivory of this lineage was supressed in favor of a proteinaceous pollen source and a carbohydrate source in the form of nectar. This association strengthened as bees became increasingly more faithful pollinators on angiosperms.

Previous Designations. Aristotle, in his *De Partibus Animalium*, had recognized bees as a distinct trophic class of insects, referring to them as "feeding on sweet saps only." Fabricius (1775) later described hymenopterans (his Class Piezata) in a key as having two pairs of maxillae (that is, a maxilla and a labium) and labial palps that were "elongated, thin, leathery." Subsequent authors have used the distinctive mouthpart structure of the maxillolabial complex as a feature of apocritan hymenopterans. Consequently the discreteness of the mouthpart class that is herein termed, glossate, has been informally recognized for some time.

The origin of the term *glossa* originates from Classical Greek and is rendered as "tongue" in English. Although seventeenth- and eighteenth-century entomologists termed many projecting, often fleshy mouthparts as tongues, the term glossa became applied formally to the median or inner lobe of the distal labium in mandibulate insects (Matsuda 1965, Denis and Bitsch 1973). (See Table 6 for history of nomenclature.) Because of the prominence and functional importance in feeding of the glossa in the mouthpart class described in this section, I am appropriating the term **glossate** in this formal and descriptive sense to characterize this mouthpart class.

Review of Literature. Several recent, major monographs have included comparative studies of mouthpart form in reconstructions of aculeate or apoid phylogeny. These studies commence with Michener's (1944) classic examination of external bee structure for reconstructing bee phylogeny; in that work cranial and mouthpart structure of major representative genera are illustrated. Brothers (1975) examined a broad sampling of structural data, including mouthparts, for establishing a phylogeny of aculeates and focused on the systematic position of the Mutillidae in particular. Later Winston (1979) conducted a study of the proboscis of long-tongued bees, including substantial data on the comparative structure of bee mouthparts. Lately two important German studies have been published, including a functional morphological study of scolioid head and mouthpart structure (Osten 1982) and a comparative morphological evaluation of the apoid postmentum for a phylogenetic reconstruction of the superfamily (Plant and Paulus 1987).

These modern works were preceded by detailed documentary studies of the comparative morphologies of the apoid maxillolabial complex (Saunders 1891, Demoll 1908), complemented by Nedel's (1960) study of the head capsule and mandible of many of the genera figured by Saunders and Demoll. Monographs on specific glossate taxa include Breithaupt's (1886) excellent study of *Apis mellifera* Linneaus, Ulrich's (1924) documentation of sphecid mouthparts and later Richards' (1962) work on vespoids, particularly masarids and eumenids. Proctor and Yeo (1973) present an informative discussion and illustrations of various vespid and apoid mouthpart structures in the context of pollination mechanisms.

Less exhaustive sources of mouthpart structure documentation are Williams' (1913) description of sphecid mouthparts, studies by Kerr and Costa Cruz (1961) and Costa Cruz (1962) on the mouthparts of *Trigona tataira* Smith that emphasized on the maxillary gland, and various contributions to the study of the honeybee, including Briant (1884), Kellogg (1902) and Strenger (1952). Janvier (1933) figured the mouthparts and briefly discussed the colletid bee *Diaphaglossa* Spinola. Grandi (1935, 1959) presented illustrations of mouthpart and head structure of various fig wasp genera. Recently Harder (1981) established a correlation between glossa length and wing length for establishing wing length as an effective field measure of the pollination capabilities of bumblebees.

THE UNIVERSITY OF CHICAGO

USE OF A PHENETIC ANALYSIS OF RECENT HEXAPOD MOUTHPARTS FOR THE DISTRIBUTION OF HEXAPOD FOOD RESOURCE GUILDS IN THE FOSSIL RECORD

VOLUME THREE

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE PHYSICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
DEPARTMENT OF GEOPHYSICAL SCIENCES

BY

CONRAD CHRISTOPHER LABANDEIRA

CHICAGO, ILLINOIS

AUGUST, 1990

8.8. Stylate-Nonhaustellate Series

8.8.1. General Features of the Stylate-Nonhaustellate Series

General Structure. The Stylate-Nonhaustellate Series consists of small to minute hexapods with stylate mouthparts that lack an ensheathing haustellum. Stylate-nonhausellae mouthparts are deployed prognathously and are housed in an oral sac that is either a primary development in parainsects (proturans, collembolans) or a secondarily derived convergence in insects (orthopterans, coleopterans) the number of stylets are two, four, six or nine and in all members the laciniae are always stylate. In the case of some proturans that bear nine stylets, virtually every available mouthpart process is stylate, including the unpaired elements of the labrum-epipharynx and hypopharynx, and the paired mandibles, galeae and laciniae (Francois 1969). Although the mandibles of members in this series are primarily or secondarily monocondylic, stylate-nonhaustellate stylets lack the lever-based protraction/retraction system that is ubiquitous in stylate-haustellate mouthparts (Smith 1985).

Unlike the presence of head- and some mouthpart-related features indicating an active, above-ground existence for stylate-haustellates (Section 8.9), stylate-nonhaustellates possess features that indicate cryptic, passive, below-ground life-habits. Associated features of stylate-nonhaustellates include the absence or dimunition of compound eyes and lack of ocelli. Unlike stylate-hautellate mouthparts, the maxillary and labial palps are well-developed, multisegmented and utile; they have not been co-opted into the formation of a haustellar sheath. Maxillary and labial appendages resemble the condition of members of the

Mandibulate Series (Section 8.3) rather than the abbreviation or frequent absence of palps that is found in the Stylate-Haustellate Series.

Included Classes. The Stylate-Nonhaustellate Mouthpart Series consists of the Entognathous-Stylate and Ectognathous-Stylate Mouthpart Classes (see Table 6 for taxal membership, life-stages and number of taxa examined for each class.)

Diversity and Other Distributional Patterns. Stylate-nonhaustellates are dimunitive, inconspicuous, minimally pigmented members of dominately subterranean, litter and fungal habitats. They are very poorly understood and only during the past 30 years have the mouthpart structures of these forms been described (Francois 1959, 1969; Schaller and Wolter 1963; Besuchet 1972, Vit 1977, 1981; Sen Gupta and Crowson 1973; Dajoz 1976; Crowson 1981; Pakaluk 1987). Their inferred diversity of approximately 1200 species from 12 families of four orders of hexapods is undoubtedly a significant underestimate. Ironically, even though stylate-haustellates are by far the least taxonomically diverse of any mouthpart series (Fig. 131), their origin from proturans, collembolans, orthopterans and three of the four suborders of coleopterans represents one of the most phyletically eclectic samples of taxa for membership in any mouthpart series. Convergence on the stylate-nonhaustellate condition has occurred at least nine times when evaluated at the familial level and includes parainsects as well as ametabolous and holometabolous insects. Within coleopterans stylate-nonhaustellates have originated independently from myxophagan, adephagan and plesiomorphic and apomorphic polyphagan lineages six times. With the possible exception of the Nontrophic Series (Section 8.10) that is characterized by numerous multiple *losses* of mouth-parts, the Stylate-Nonhaustellate Series possesses the greatest number of phyletic convergence events toward the *acquisition* of any mouthpart type.

Insight into the origin of a stylate-nonhaustellate mouthpart type from an unspecified mandibulate type is provided by Dajoz's (1976) description of a transformation series culminating in stylate-nonhaustellate taxa within the coleopteran family, Cerylonidae. A similar series may exist for taxa within the collembolan family Neanuridae. Although other transitional types between mouthpart classes or series have been cited (e.g. *Nannochorista* for the rostrate/labellate transition), the transformation sequence documented by Dajoz offers the best example of a major mouthpart transitional type.

Although only 17 taxa were examined, certain conclusions can be made regarding the dietary repertoire of stylate-nonhaustellates. Stylate-nonhaustellates are almost exclusively fungivorous, consuming principally mycelia, but also spores and sporocarps (Sturm 1959, Crowson 1981); there is some evidence for detritivory (Wolter 1963) as well as indirect consumption of bacteria and protistans (Moore 1988). Their overall size and stylet structure indicate that they can puncture individual mycelial cells for evacuation of their contents (Crowson 1981, Moore 1988). Often stylate-nonhaustellates occur with small, fungivorous adult-ectognathate beetles (e.g. Wheeler 1984, Ashe 1984b) in large, ephemeral sporocarps and plasmodia in litter. The recently discovered, enigmatic orthopteran, *Cooloola propator* Rentz 1980, is an exception and is apparently a fossorial predator (Rentz 1987).

Major Structural Variations. When compared to the structural differences among mouthpart classes of other mouthpart series, no major structural variation can be discerned between the two constituent mouthpart classes within the Stylate-Nonhaustellate Mouthpart Series.

Geochronologic Range. The geochronologic history of the Stylate-Nonhaustellate Series is minimally documented by the fossil record, although sister-group relationships with taxa possessing better fossil records assist in inferences regarding the timing of origin of several lineages. The geochronology of stylate-nonhaustellates is described by two, temporally disjunct diversifications involving unrelated hexapod lineages. The first was an early, Silurian or earliest Devonian diversification of collembolan and presumably proturan forms as detritivores and fungivores among the earliest, primitive, terrestrial communities (Labandeira and Beall 1990, Shear 1990). The second diversification was an Early to Middle Mesozoic appearance of at least five or six lineages of coleopterans and an orthopteran lineage in highly-structured terrestrial communities.

Evidence for the Siluro-Devonian emergence of proturans and neanurid collembolans originate from the presence of Early Devonian entognathate collembolans and a sister-group relationship between the Collembola and the entognathous-stylate Protura (Kristensen 1981, Boudreaux 1987) and the probable presence of a stylate neanurid collembolan from the Lower Devonian Rhynie Chert [104] (Delamare-Deboutteville and Massoud 1967, Greenslade 1988). Previous workers considered this fossil a poduromorph collembolan (Tillyard 1928, Scourfield 1940, Massoud 1967), although current evidence indicates that its mouthparts were stylate (Greenslade 1986). Available food resources for these early, cryptic stylate-nonhaustellates include algae, fungi, decomposing vascular plant material and dead arthropods (Kidston and Lang 1921a,b; Kevan, Chaloner and Savile 1975; Selden and Edwards 1989). Based on habitat occurrences of modern relatives, these forms presumably were litter-inhabitants or possibly fossorial.

The emergence during the Mesozoic of the second wave of stylate-nonhaustellates is ironically more difficult to assess. The timing of this diversification may be coincident with the origin of a major novel fungal food resource, but it is uncertain what fungal group originated during this time (see Taylor 1990). Possible candidates include root mycorhizae and large, fleshy sporocarps of ascomycetous and basidiomycetous fungi. Alternatively, ectognathous-stylate taxa may have exploited an adaptive zone (*sensu* Van Valen 1971) such as ephemeral, terrestrial sporocarps that was not previously colonized.

8.8.2. Entognathous-Stylate Class (Class 22)

Description. Head quadrate, proboscate; prothoracic legs often antenna-like. Genae prominent; gular area moderately developed. Mouthparts symmetrical, entognathous, protractile and stylate-nonhaustellate; stylet number 2, 6 or 9.

Clypeus transversely elongated, subsegmented. Labrum quadrate or transversely elongate, single, margin acute or acuminate. Hypopharynx often styliform; epipharynx variable. Mandibles monocondylous; mostly stylate and edentate; musculation of protraction/retraction. Maxillae bearing two basal sclerites and galeae, laciniae and palps, or bearing laciniae only. Maxillary palps 4- or 5-segmented, pectinate, short, or absent. Galeae often stylate (either singly or doubly pronged); laciniae always stylate-acuminate. Labium prolonged with 3 basal segments and median ligulate structure and palps. Labial palps 1- or 2-segmented, stubby or intermediate in length; infrequently absent. Glossae and paraglossae forming an oral cone, or less commonly are generalized lobes. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. The most distinctive feature of entognathous-stylates is the combined presence of entognathy and nonhaustellate, stylate mouthparts. Unique features are the absence or minimal development of compound eyes and a prolonged, acutely- to acuminately-tipped labrum. Features found in most entognathous-stylates and atypical or absent in other mouthpart classes include tactile, forwardly-directed prothoracic legs in lieu of antennae, a double-bladed lacinial stylet and paraglossae/glossae forming a labial cone.

Entognathous-stylate mouthparts are separated from ectognathous-stylate mouthparts (Section 8.8.3) by the presence of entognathy, a transverse clypeus, an acuminately- to acutely-margined labrum and poorly developed or absent eyes. Entognathous-stylates differ from entognathates (Section 8.3.2) by the presence of styliform mouthparts that always include the laciniae and frequently the epipharynx/labrum, mandibles and galeae.

Diversity and Natural History. The dominant habitats of entognathous-stylates are the hypogean or epigean zones of moist soil, litter, humus, moss, decaying wood and bark (Eisenbeis and Wichard 1987, Moore 1988). This mouthpart class comprises the order Protura with four constituent families and the family Neanuridae of the order Collembola. These five families collectively represent a species diversity of 520 (Appendix D), corresponding to a rank-order of 30 among the 34 mouthpart classes (Table 5, Fig. 131). Thus the contribution of entognathous-stylates to overall mouthpart abundance is negligable, although they are a structurally intriguing group of small (0.5 to 2.5mm), unpigmented, piercing-and-sucking arthropods adapted to cryptic, often overlooked habitats (Richards and Davies 1977). Entognathous-stylates are very poorly known; proturans were only discovered in 1907 by Silvestri and most data regarding their natural history has been deduced from occasional anecdotal observations of diet, laboratory rearings of "acclimated" species feeding on diets grown on culture media and, most recently, trophic web analyses of endogean microarthropod systems (Moore 1988).

Much of what is known about the diets of entognathous-stylates has focused on neanurid collembolans rather than proturans, principally because of the greater abundance and larger size of collembolans (Joosse 1983). Proturans are apparently fluid-feeders on fungal hyphae and possibly bacteria (Eisenbeis and Wichard 1987) (Fig. 92), including ectomycorhizae in oak forest soils (Moore 1988). Proturans inhabit the interstices among soil particles in locally high densities from three to ten cm from the soil surface. They prefer high humidities and

CLASS 22: ENTOGNATHOUS-STYLATE

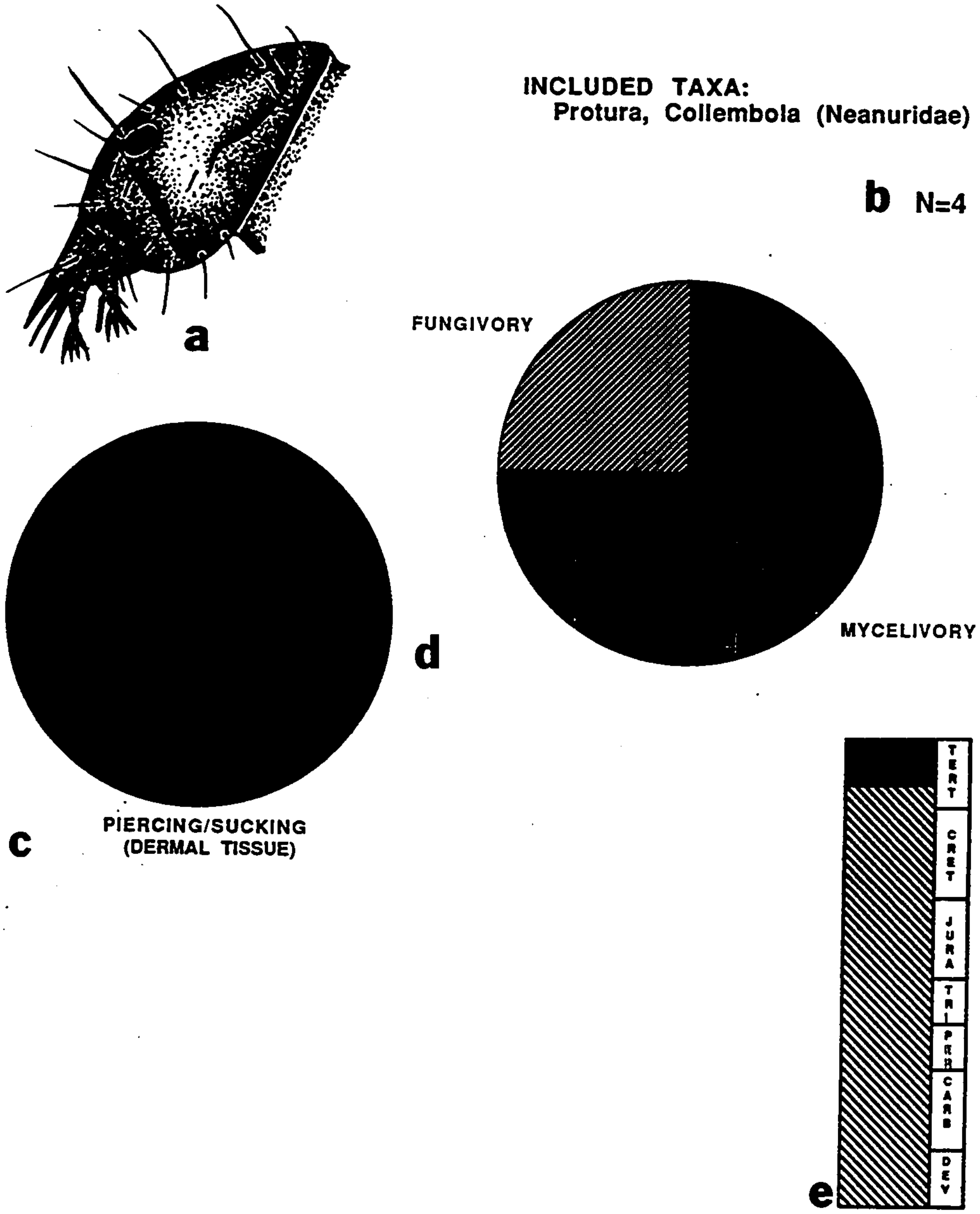


FIGURE 92. Overview of the Entognathous-Stylate Mouthpart Class. a, *Acerentomon doderoi* Silvestri (Protura: Acerentomidae, data-set no. 1), after Francois 1969; b, taxonomic distribution and number of taxa examined; c, functional-feeding-group; d, dietary spectrum; e, geochronologic range.

temperatures and probably play a salient role in recycling fungal-bound nutrients to the ambient substrate.

Neanurid collembolans, like other collembolans, occur in the soil, decaying litter, moss, and, perhaps the only above-ground habitat, under tree bark (McNamara 1924, Wolter, 1963, Hamilton 1978). Although collembolans as a group are saprophages and phytophages chewing and ingesting fungal spores, mycelial fragments, pollen grains, algal filaments and cellulosic fragments of higher plants (Poole 1959, Christiansen 1964, Verhoef et al. 1988), Christiansen (1964: 153) claimed that "We know nothing about the diet of forms with piercing or sucking mouthparts." Previously McNamara (1924) considered *Neanura muscorum* (Templeton) a fluid-feeder because of the lack of visible gut contents, a conclusion which Poole (1959) corroborated by citing the absence of a grinding molar region on the mandible as additional supportive evidence. Wolter, in an important discussion of the piercing-and-sucking apparatus of *N. muscorum* (1963: 58) stated that this species fed on mucilaginous fungi and pine wood ("*Neanura muscorum an gelben schliemigen Pilzen aur Kiefernholz saugend.*") and indicated that the hook-like, elongate mandibles act as grapplers to bring mycelia toward the gnathal pouch where they are pierced by the maxillary stylets for fluid feeding. (This system has also been detiled for the ectognathous-stylate beetle *Hoplocnema sallaei* Matthews by Pakaluk [1987].)

The role of a fungivorous-dominated community of subterranean piercing-and-sucking arthropods feeding often on vesicular-abrbuscular mycorhizae has been discussed by Moore (1988) in terms of a symbiotic mutualism. According to Moore (1988), high densities of these fluid-

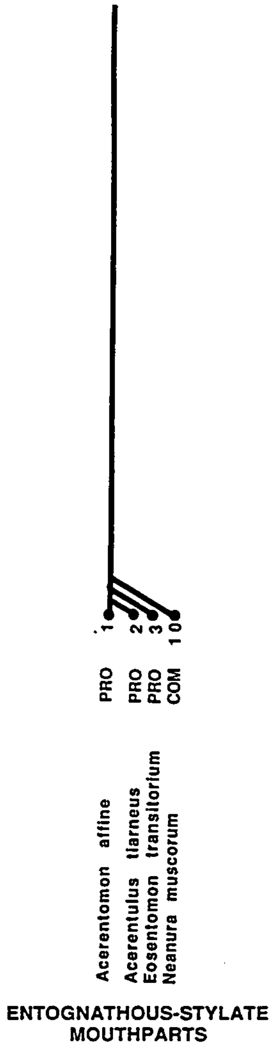


FIGURE 93. Cluster analysis dendrogram of taxa comprising the Entognathous-Stylate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

feeding fungivores (including many mite taxa) can stimulate fungal growth, disperse spores and act as vectors for innoculation of mycorhizae. In turn mycorhizae provide an important food resource for the fungivores. Other possible associations of entognathous-stylates need to be assessed. These include the degree to which hypogean animal tissue such as nematodes, rotifers and other microarthropods are consumed and the extent of piercing-and-sucking of individual plant cells such as those found in algal filaments, mosses and possibly minute vascular plants in hypogean and epigean habitats.

Structural Themes. No major structural themes are evident from the dendrogram of the entognathous-stylate mouthpart class (Fig. 93).

Geochronologic History. Entognathous-stylates lack a fossil record (Fig. 94), with the possible exception of a neanurid collembolan in the Lower Devonian of Scotland [104] (Greenslade 1988). This depauperate record is attributable to their small to very small size, lack of highly preservable, sclerotized structures such as wings and occurrence in sedimentary environments unlikely to enter the geological record. Entognath collembolans (Section 8.3.2) have a fossil record of at least ten occurrences (Fig. 31). Because of this fossil record, including presence of an Early Devonian arthropleonan collembolan, the existence of the sister-group of the Collembola, the Protura, can be inferred to have been present during the Early Devonian. Collembola and Protura share at least six synapomorphies (Kristensen 1981) and repeated analyses of primitive hexapod relationships have resulted in conclusions supporting a sister-group relationship between the two taxa (Boettger

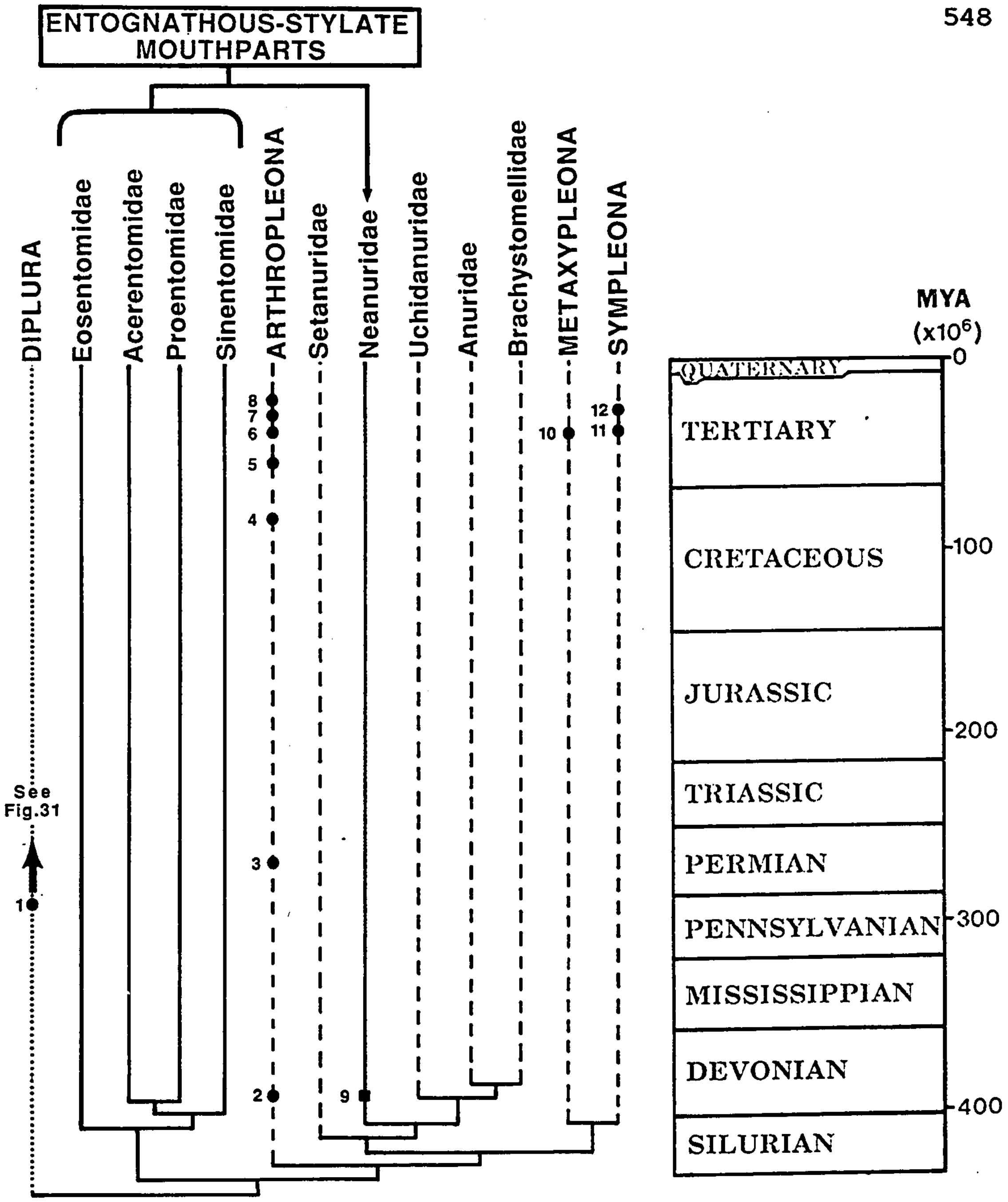


FIGURE 94. Geochronologic history of the Entognathous-Stylate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Schaller (1970), Janetschek (1970) and Kristensen (1981). The taxonomic level of analysis is the family or suborder. The Protura lack a fossil record. The outgroup is Diplura. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

1958, Tuxen 1971, Lauterbach 1972, Labandeira et al., in prep.). Most of these studies have also concluded that, whereas the Protura, Collembola and Diplura (=Parainsecta) are plesiomorphic with regard to the Insecta, they nevertheless exhibit many apomorphies concomitant with a specialized, cryptozoic and fungivorous life-habits.

From this it can be concluded that entognathous-stylates originated very early as a mouthpart class and is at least as old or older than entognathates, monocondylates and adult-ectognathates. This early occurrence is consistent with Ghilarov's (1956) hypothesis that the ancestral hexapod habit was hypogean and that tracheates became terrestrialized as supralittoral psammon (Labandeira and Beall 1990). Entognathous-stylates preceded functionally analogous ectognathous-stylates by approximately 200 million years, occupying a feeding niche that apparently was only reinvaded during the Mesozoic.

Previous Designations. After a study of the basal hexapod groups, Tuxen (1959) united the Protura, Collembola and Diplura into the hexapod Entognatha. (This corresponds to the Parainsecta of Table 1.) The Entognatha were unified by mouthparts placed in an oral sac that was formed by the lateral and ventral extension of the cephalic capsular wall and thus enclosing ventrally-located mouthparts by medial fusion. By extension, all other hexapods, i.e. insects, became known as ectognaths. Subsequently the term entognath has referred to mouthpart placement in noninsectan hexapods. Chaudonneret (1989a) recognized this mouthpart class as a "*l'appareil piquer de certains Aptérygotes entotrophes*," which included proturans and possibly some collembolans and was described as a major piercing mouthpart type (See Table 6 for further details of the history of nomenclature). Since the mouthpart type described in this section also bears stylate mouthparts, the term **entognathous-stylate** uniquely refers to this discrete mouthpart class. This designation has not been previously used.

Review of Literature. Studies of entognathous-stylate mouthparts primarily have been limited to only two exhaustive examinations of proturan mouthparts and a single study of neanurid mouthparts. The head and mouthpart structure of the proturan *Acerentomon propinquum* (Condé) was extensively documented by Francois (1959)--the first monographic account of a stylate-nonhaustellate mouthpart type. Francois later (1969) examined *Acerentomon affine* Bagnall and *Eosentomon transitorium* Berlese, much in the same detailed and exhaustive manner as before. Tuxen (1959) meanwhile provided a wide-ranging account of mouthpart structure in all three entognath orders. Finally, Schaller and Wolter (1963) and Wolter (1963) conducted an extensive inquiry into mouthpart structure and function, digestive tract anatomy and dietary regime of the neanurid collembolan *Neanura muscorum* (Templeton). Excellent scanning electron micrographs of proturan mouthparts can be found in Eisenbeis and Wichard (1987).

8.8.3. Ectognathous-Stylate Class (Class 23)

Description. Head quadrate, symmetrical, with proboscis of variable length; anterior prolongation of thorax enveloping dorsal head area in some. Genae prominent; gula well-developed, infrequently absent.

Antennae variable; ocelli mostly absent; compound eyes moderately developed, dichoptic. Food pump pharyngeal, with or without clypeal pump. Mouthparts stylate-nonhaustellate, prognathous to rarely hypognathous, with 4, 6 or rarely 2 stylets; stylets generally protractile.

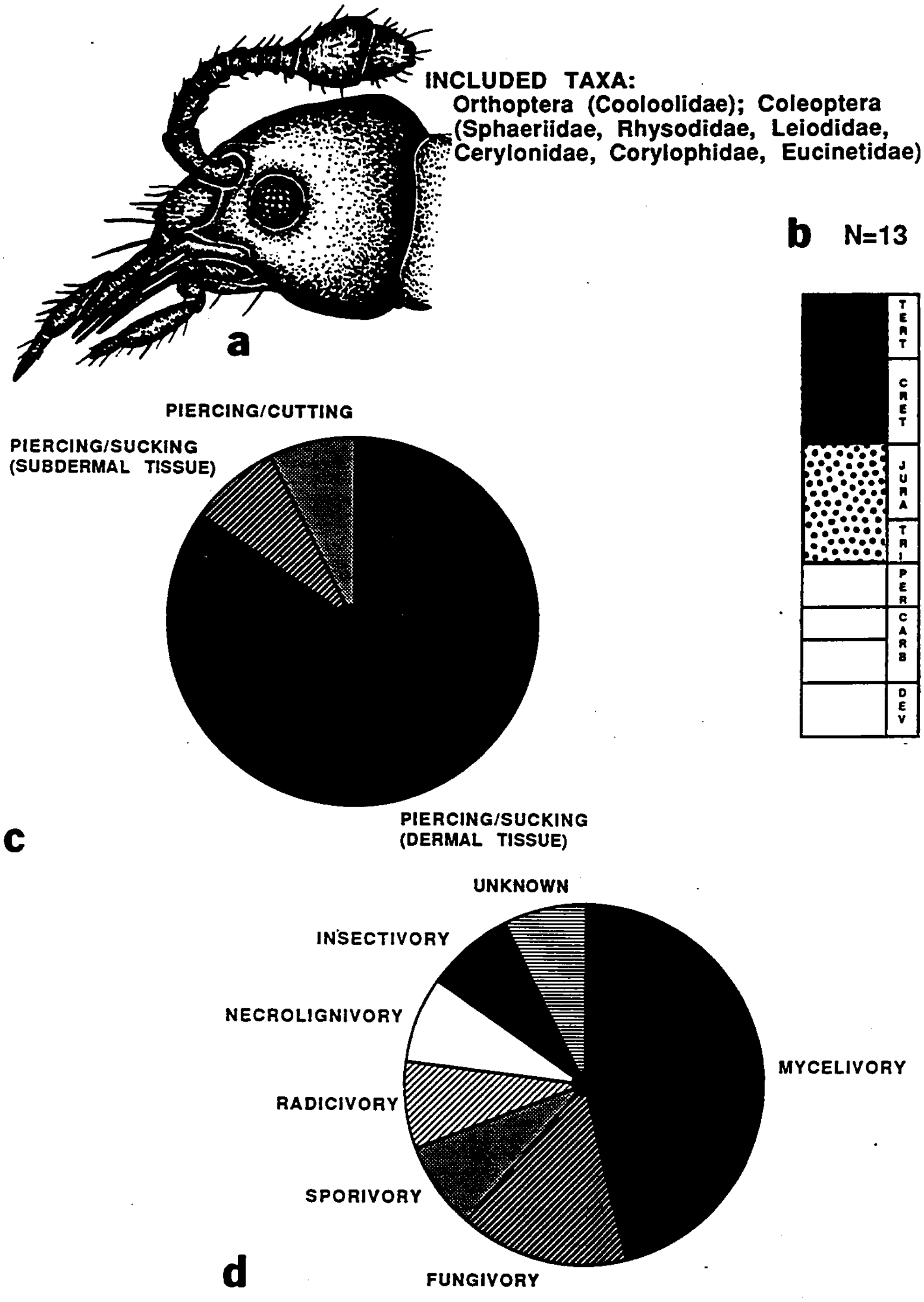
Clypeus single or fused to frons, shape variable. Labrum single (rarely absent), shape variable, margin a beak brace. Hypopharynx variable; epipharynx generally a sensory organ and beak brace, or absent. Mandibles secondarily monocondylic or rarely absent; stylate to less commonly tetragonal; edentate, often with a stylate prostheca; musculation characterized by protraction/retraction. Maxillae often with elongated stipes for stylet protraction; bearing galeae, laciniae and palps. Maxillary palps generally 4-segmented, long; filiform or with an enlarged middle segment. Galeae often stylate, rarely absent; laciniae always stylate. Labium generally producing a ligula and palps. Labial palps 3-segmented, intermediate in length, filiform or with enlarged middle segment: Glossae forming a labral cone, generalized or mucronate, rarely absent. Paraglossae mostly absent. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. A basic feature distinguishing ectognathous-stylate mouthparts from other mouthparts, particularly entognathous-stylate mouthparts (Section 8.8.2), is the joint presence of ectognathy and stylate mouthparts. Unlike the nine mouthpart classes in the Stylate-Haustellate Series (Section 8.9), ectognathous-stylate mouthparts lack an enveloping sheath, or haustellum, that protects the stylate mouthparts from the external environment. The presence of stylate mouthpart elements in the form of mandibular, galeal or lacinial stylets differentiates ectognathous-stylate mouthparts from adult-ectognathate mouthparts (Section 8.3.4).

Since confusion may arise in separating key features of ectognathous-stylate and entognathous-stylate mouthparts, the following features are important. Whereas compound eyes are well-developed in ectognathous-stylates, they are rudimentary or absent in entognathous-stylates. The labrum, epipharynx and hypopharynx are not stylate or stylet-associated structures in ectognathous-stylates whereas they are in most entognathous-stylates. The lacinia, when stylate, consists of one blade in ectognathous-stylates and mostly consists of two blades (proturans) in entognathous-stylates. Both maxillary and labial palps are relatively long and rarely short in ectognathous-stylates and short, often stubby in entognathous-stylates. Finally, the paraglossae are unmodified or absent in ectognathous-stylates, and mostly contribute to formation of an oral cone in entognathous-stylates.

Diversity and Natural History. Ectognathous-stylates comprise an important component of the microarthropod litter fauna and, with one exception, consist of small to very small (generally 0.3 to 3mm long) beetles. Ectognathous-stylates are members from seven families representing an estimated species diversity of 670 (Appendix D), corresponding to a rank-order of 28 among the 34 mouthpart classes (Table 5, Fig. 131). When considered at the family level, the ectognathous-stylate condition originated at least seven times, six within the Coleoptera and once within the Orthoptera. When evaluated at the infrafamilial level, a more realistic value for the amount of convergence is at least double this value (Lawrence and Stephan 1975, Pakaluk 1987). Ectognathous-stylates taxonomically comprise several coleopterans from the myxophagan family Sphaeriidae, the adephagan Rhysodidae and the polyphagan families Leiodidae (not evaluated in this study), Eucinetidae, Cerylonidae and Corylophidae, and the orthopteran family Coolooidae. However, because of the usually small size of these insects, their occurrence in inconspicuous and cryptic habitats and the fact that most taxa have been described only within the past 20 years, ectognathous-stylates are poorly known and it is probable that other examples among poorly understood, cryptic coleopteran families will be discovered. Curiously, there is only one known example of stylate mouthparts within any of the several orthopteroid orders.

Ectognathous-stylates are characterized by the possession of one to four pairs of stylate mouthpart elements that are enclosed by a channeled labium and/or labrum, which is used for piercing individual fungal hyphae, algal filaments and doubtfully animal tissue (Crowson 1981). Most forms consume fungi (Fig. 95) and ultimately depend on wood for their existence since wood is a substrate for growth of a diverse suite of fungi. Thus ectognathous-stylates, as fungivores, are an essential link in a tripartite partnership among fungus beetles, fungi and woody vascular plants (Crowson 1981). The most productive components of the decaying wood/leaf litter habitat are bacteria and fungi, and fungi in the form of single cells and septate or aseptate hyphae that form the basic food resources of ectognathous-stylates (Kukor and



INCLUDED TAXA:
Orthoptera (Cooloolidae); Coleoptera (Sphaeriidae, Rhysodidae, Leiodidae, Cerylonidae, Corylophidae, Eucinetidae)

FIGURE 95. Overview of the Ectognathous-Stylate Mouthpart Class. a, *Cautomus sugerens* Besuchet (Coleoptera: Cerylonidae, data-set no. 626), after Besuchet (1972); b, taxonomic distribution, numbers of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

Martin 1987). Ectognathous stylates are associated with concealed, "microscopic" spore- and hyphal-producers and less commonly with conspicuous, "macroscopic" structures such as basidiomycete sporocarps that typically harbor larger insects, especially those of the adult-ectognathate class (Ashe 1984b; Wheeler and Blackwell 1984).

A broad range of major fungal taxa are consumed by entognathous-stylates. Cerylonids are associated with bark, plant detritus, nests and endogean habitats (Besuchet 1972, Crowson 1981, Willemstein 1987); Australian forms feed on the plasmodial phase of myxomycetan fungi (Slipinski 1988). Claims of cerylonid ectognathatous-stylates preying on larval insects (Besuchet 1972) are considered unlikely by Lawrence and Stephan (1975), who recovered hyphal fragments and spores from the gut contents of cerylonids inhabiting rotten cambial wood and leaf litter. Corylophids are inhabitants of rotting vegetation and decaying wood (Willemstein 1987) and are known to contain dematiaceous deteuromycetes as gut contents (Pakaluk 1987). Stylate-nonhaustellate leiodids (not documented in this study) apparently feed on subterranean ascomycetes (Willemstein 1987) and are members of the litter fauna (Crowson 1981). Eucinetids from Brazil, Turkey and Japan included saproxylophagous forms occurring on polypore fungi, mosses, decomposed wood and in galleries of bark engraver weevils (Vit 1977). Rhyosidids and sphaeriids (Pauly 1915) are probably feeders on fungal hyphae or algal filaments (Crowson 1981). The only atypical diet of this mouthpart class is a fossorial Australian cooloolid, an orthopteran that is apparently insectivorous (Rentz 1980, 1987).

Ectognathous-stylate mouthparts present some interesting evolutionary and ecological developments aside from their diets. Studies of stylate beetles provide one of the few examples of a complete morphologic transformation series between typical mandibulate forms and specialized stylate forms. These series, with amply documented transitional forms, are demonstrated in eucinetids (Vit 1977) and cerylonids (Sen Gupta and Crowson 1973, Lawrence and Stephan 1975, Dajoz 1976) and may exist for other families. Additionally, cerylonids are one of the few holometabolous groups in which *both* an adult and a larva possess the same specialized, stylate mouthparts, indicating that both life-cycle stages have become adapted to the same, spatiotemporally restricted habitat (Crowson 1981). Generally mouthpart structures in ectognathous-stylates have functional parallels among entognathous-stylates (Section 8.8.2) and, in addition to piercing, both groups possess stylate mouthpart elements bearing processes for pulling hyphae or wood fibers toward their oral chambers (Wolter 1963, Pakaluk 1987).

Structural Themes. Five major structurally-based subclusters exist for entognathous-stylate mouthparts (Fig. 96). The subclusters are (i) the single adult orthopterid, *Cooloola propator* Rentz (data-set entry no. 98 of Fig. 96), (ii) an adult myxophagan/adephagan subcluster of five members (401-499), (iii) an adult polyphagan cerylonid subcluster of five members (624-627), (iv) the single adult polyphagan corylophid *Hoplocnema sallaei* Matthews (633) and (v) a polyphagan subcluster comprising the single larval cerylonid *Philothermus bicavis* Sharp (631). Although these five subclusters are discrete within the mouthpart class

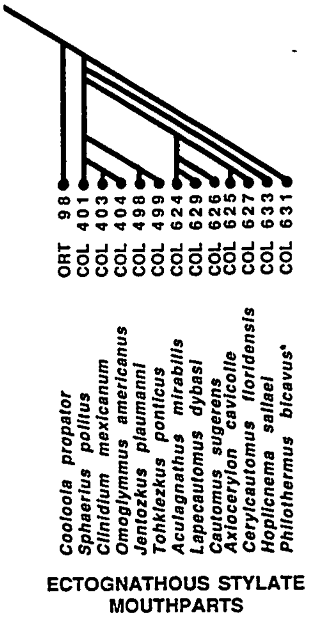

ORT 98 Cooloola propator
COL 401 Sphaerius pollitus
COL 403 Clinidium mexicanum
COL 404 Omoglymmus americanus
COL 498 Jentozkus plaumanni
COL 499 Tohklezkus ponticus
COL 624 Aculagnathus mirabilis
COL 629 Lapecautomus dybasi
COL 626 Cautomus sugerens
COL 625 Axiocerylon cavicolle
COL 627 Cerylcautomus floridensis
COL 633 Hoplicnema sallaei
COL 631 Philothermus bicavus*
ECTOGNATHOUS STYLATE
MOUTHPARTS

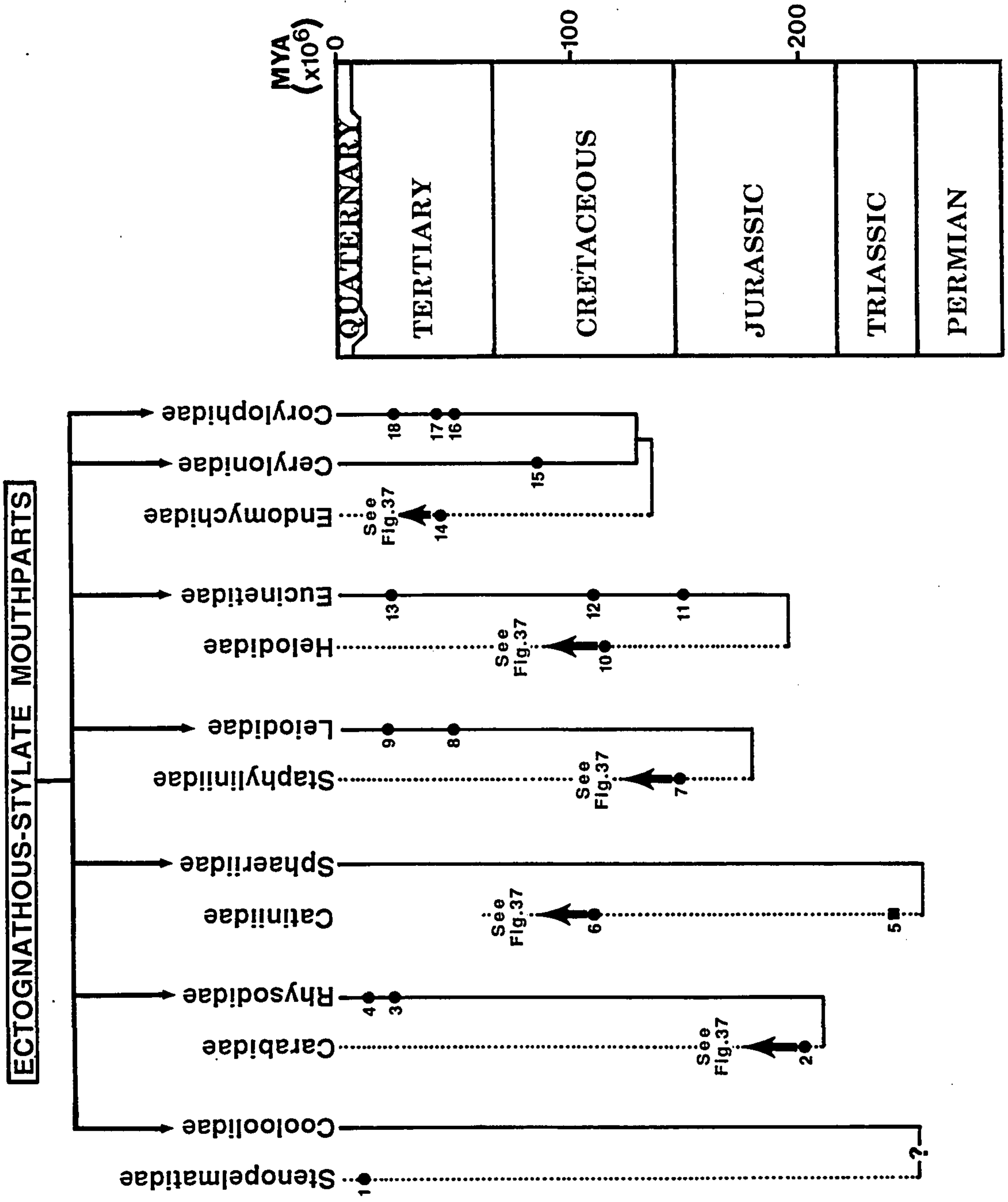
FIGURE 96. Cluster analysis dendrogram of taxa comprising the Ectognathous-Stylate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

by comparison to dendrograms of other, more diverse classes, subclustering among ectognathous-stylates is less pronounced.

These structural themes are largely attributable to several major character-state complexes and character-states. The most important is an orthopterid (*Cooloola*) versus a coleopterid (all others) head and mouthpart facies. Another difference involves whether a larval coleopteran facies (*Philothermus*) or an adult coleopteran facies is present. The third dichotomy concerns the number of mouthpart elements as stylets, that is whether they are two, four or six; as well as which mouthpart elements contribute to stylet formation (mandibular, galeal, lacinial or a combination thereof). The structure of the epipharynx and hypopharynx also contributes to the formation of subclusters, as does labial palp structure, particularly since many tenebrionoid (=heteromeran) families bear labial palps with enlarged middle segments.

Geochronologic History. Ectognathous-stylates have a poor fossil record, as does their adult-ectognathate sister-groups (Fig. 97). Connsequently, based on the distribution of rare fossil forms and occasionally uncorroborated phylogenetic relationships of ectognathous-stylate lineages and their sister-groups, any inferences must be necesarilly tentative. The bizarre, monotypic orthopteran family Cooloolidae lacks a fossil record, although its closest relatives are probably the Stenopelmatidae (Rentz 1980, 1987). Stenopelmatids occur relatively recently in the Lower Miocene [5] (Zeuner 1939) even though they are probably a Late Paleozoic group originating before the breakup of Pangaea (Vickery 1989).

FIGURE 97. Geochronologic history of the Ectognathous-Stylate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylograms are after Crowson (1981), Lawrence and Newton (1982) and suggestions by Rentz (1980, 1987). The taxonomic level of analysis is the family. The outgroups are Stenopelmatidae, Carabidae, Catiniidae, Staphylinidae, Helodidae and Endomychidae. Relevant members of the Leiodidae were not analyzed in this study but undoubtedly are ectognathous-stylate members. The Cooloolidae lacks a fossil record. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.


ECTOGNATHOUS-STYLATE MOUTHPARTS
MYA
(x10^6)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
Corylophidae
18
17
16
Cerylonidae
15
Endomychidae
See Fig.37
14
Eucinetidae
13
12
11
Helodidae
See Fig.37
10
Leiodidae
9
8
Staphylinidae
See Fig.37
7
Sphaeriidae
Catiniidae
See Fig.37
6
5
Rhysodidae
4
3
Carabidae
See Fig.37
2
Coolooliidae
?
Stenopelmatidae
1

Rhysodids are probably an ancient adephagan group (Crowson 1955) that lack a Mesozoic record and presently occur under bark (Hamilton 1978, Crowson 1981). Their sister-group, the diverse Carabidae, have a prolific fossil record (Crowson 1974) and have their earliest fossil occurrence as unnamed forms from the Lower Jurassic of England [69] (Whalley 1985). The earliest rhysodid occurs in Upper Eocene to Lower Miocene Dominican amber [17] (Baroni-Urbani and Saunders 1982). Myxophagans are small inconspicuous forms that virtually have a nonexistant fossil record. Myxophagan sphaeriidids lack a fossil record and their sister-group, the Mesozoic Catiniidae, has a doubtful first occurrence in the Early Triassic of Asia [82] (Ponomarenko 1969) although a catiniid occurs in the Lower Cretaceous of the USSR [52] (Rasnitsyn 1988). Leiodids do not appear as credible fossils until the Lower Tertiary (Dmitriev and Zherikin 1988) and an occurrence has been noted by Schumann and Wendt (1989) in Early Miocene amber [6]. Their sister-group, the diverse Staphylinidae, has an earliest occurrence as *Porrhodromus communis* Tichomirova 1968 in Upper Jurassic deposits of the USSR [60]. Unassigned eucinetids are also known from these same deposits [60] (Crowson et al. 1967, Rasnitsyn 1988), although the earliest occurrence of their sister-group, the Helodidae, has a younger earliest occurrence in the Lower Cretaceous of Australia [53] (Jell and Duncan 1986). Crowson (1981) indicates a mid-Jurassic divergence for these two groups. Cerylonidae and Corylophidae are sister-groups that share the Endomychidae as an outgroup. The earliest occurrence of an endomychid is in Baltic amber [19] and is of no use in establishing the origin of the Cerylonidae + Corylophidae, although Crowson (1981) places their divergence from the Endomychidae during the Early Cretaceous.

In summary it appears that ectognathous-stylate mouthparts arose sporadically throughout the Mesozoic in various coleopteran groups and once among orthopterans. This tentative pattern does not suggest a geochronologically rapid radiation into a newly-created adaptive zone (cf. Van Valen 1971), but rather repeated invasions by relatively nondiverse groups into an adaptive zone that probably arose during the Late Paleozoic (Malyshev 1968, Hamilton 1978, Taylor 1990).

Previous Designations. Three conditions collectively and uniquely define the mouthpart class defined herein: (i) lack of a haustellum, (ii) ectognathy and (iii) stylate mouthparts. The lack of a haustellum is referred to under the mouthpart series to which this and the previously described mouthpart class (Section 8.8.2) are a constituent members. The other two features are used to derive the namesake of this mouthpart class: **ectognathous-stylate.** The term, ectognathous-stylate, is a novel designation and has not been used previously in the entomological literature. Neither Matsuda (1965), Bitsch and Denis (1973) or Smith (1985) discussed ectognathous-stylates (Table 6). Chaudonneret (1989a) however considered "*l'appareil piqueur de certains Coléoptères adultes*" as a distinctive piercing mouthpart type and used *Jentozkus plaumanni* Vit as illustrative of this mouthpart type.

Review of Literature. Of the several ectognathous-stylate families that have been studied, an overwhelming effort has been devoted to the taxonomy and description of the mouthpart structure of the

Cerylonidae. Besuchet (1972) was the first to extensively document cerylonid mouthpart structure. This was followed by Sen Gupta and Crowson (1973), Lawrence and Stephan (1975) and Dajoz (1976), who revised the taxonomic limits of the family, described additional species and figured additional mouthpart transformation series from mandibulate to completely stylate species. Slipinsky (1988) has provided descriptions and accounts of the habitat of Australian species. Pakaluk (1987) has described the stylate mouthparts and diets of a corylophid, a closely related family.

Other data sources for stylate beetles include Vit (1977, 1981) for species of the Eucinetidae and Pauly (1915) who figured rhysodid mouthpart structure in a monograph on caraboid head and mouthpart structure. This work was complemented by Stickney's monograph on coleopteran head structure that included rhysodids. Lastly a recent contribution has been made by Rentz (1980, 1987) on the unusual stylate mouthparts of a new family of fossorial orthopterans.

8.9. Stylate-Haustellate Series

8.9.1. General Features of the Stylate-Haustellate Series

General Structure. The Stylate-Haustellate Series consists of a very diverse group of nine mouthpart classes united by the common presence of an organ bearing stylets or modified into a stylet for puncturing and obtaining food from integumentally-bound tissue. This organ (haustellum) is variously deployed hypognathously, opisthognagously or rarely prognathously and may be retractile or nonretractile. The number of haustellar stylets is as many as six (hexastylates), although two (buccal-cone, monostylate/distylate, distylate/tetrastylate), three (mouthcone, tristylate) or four (segmented-beak, distylate/tetrastylate) are common and one (monostylate/distylate, tubulostylate, siphonostylate) is relatively rare. The mouthpart element identities of the stylets range from single epipharyngeal and hypopharyngeal stylets, to a single or paired mandibular stylet(s), to paired lacinial stylets. In the majority of groups styliform mouthpart elements are dominated by protractor and retractor muscles, often with the assistance of various internal sclerite/muscle lever mechanisms, for assisting retraction by increasing stroke efficiency and stroke throw. Stylate-haustellate piercing elements are longer, more gracile and more elaborately dentate than analogous or homologous mouthpart elements of the Stylate-Nonhaustellate Series (Section 8.8). An associated feature of stylate-haustellate mouthparts is palpal modification, specifically a trend toward reduction, elimination or often transformation of labial palps into a haustellum that partially or completely ensheaths the mouthpart stylets. Also, labra are often prolonged, either in conjunction with a beak brace or as a dorsal surface of an epipharyngeal stylet. Intimately associated with haustellate mouthparts and a general piercing-and-sucking mode of feeding (or some modification thereof) is an inflated, enlarged, clypeal region with dilator muscles that operate as a sucking pump. Because of the diversity of fluid diets, occupied habitats and life-histories of stylate-haustellates, few head-associated features can be consistently encountered in the series.

While the stylate mouthparts of all nine classes function in a similar way of penetrating integument to obtain fluid food from subjacent shallow or deep tissue, there are many modifications of this basic theme. The most common mode of obtaining fluid nutriment is by piercing-and-sucking, in which stylets (or a stylet) puncture integument and variously penetrate subdermal tissue by a gently applied but sufficient force (Pollard 1973, Dixon 1975). A second mechanism is the slash-and-cutting tecnhique of some hexastylates (Gordon and Crewe 1953, Dickerson and Lavoipierre 1959) in which serrated, bladelike mandibles cut and lacerate integument and underlying surface tissue and the resulting pool of fluid (e.g. blood, lymph) is sucked up through a haustellum. Alternatively the punch-and-sucking technique of the mouthcone class is characterized by punching a hole on the wall of a pollen or spore grain by a stout mandibular stylet, followed by lacinial enlargment, deepening of the hole and subsequent sucking out of the pollen or spore contents (Grinfel'd 1959; Kirk 1984, 1987). A similar mechanism has been documented for the evacuation of individual cellular contents of leaf tissue (Chisholm and Lewis 1984), Weisenborn and Morse 1988). Lastly, many blood-feeding and insectivorous classes have a thrust-and-stab technique, by which considerable force is used to "propel" a stiffened stylet for obtaining sufficient penetration to puncture through an integument (Bänziger 1980). This behavior is followed by location of a blood capillary or blood sinus for discharge of anticoagulant enzymes, or injection of various lytic enzymes for liquefaction of prey contents (Scarbrough 1978). These four functional modes of obtaining fluid food illustrate some of the major modifications that stylate-haustellate mouthparts have evolved to obtain fluid food in differing contexts of tissue types and integumental structure.

Included Classes. The Stylate-Haustellate Series consists of the Segmented Beak, Buccal-Cone, Mouthcone, Monostylate/Distylate, Distylate/Tetrastylate, Hexastylate, Tristylate, Tubulostylate and Siphonostylate Mouthpart Classes (see Table 6 for taxal membership, life-stages and number of taxa examined for each class).

Diversity and Other Distributional Patterns. The Stylate-Haustellate Series comprises a very taxonomically diverse assemblage of mouthpart classes and is surpassed by species diversity only by the Mandibulate and Siphonate Series. Represented are 115,000 species from eight orders of hemimetabolous and holometabolous insects, of which 70% of the species are segmented-beaks (Section 8.9.2). However, since the Siphonate Series comprises only two mouthpart classes and is dominated by the single, highly stereotyped Siphonate Mouthpart Class (Section 8.6.2), the Stylate-Haustellate Series is significantly more diverse in terms of mouthpart class diversity and is second only to the Mandibulate Series (Section 8.3). When evaluated at the ordinal level, insects have converged on this mouthpart series at least seven times: hemipterans (Homoptera + Heteroptera), thysanopterans, anoplurans, mallophagans (Haematomyzidae), dipterans, siphonapterans and lepidopterans.

Stylate-haustellates inhabit virtually every terrestrial and freshwater habitat and occur in open marine settings (Andersen and Polhemius 1976). They consume fluid foods from every kingdom of organisms, principally plants and animals, but also fungi (Kukor and

Martin 1987) and modified filter-feeding on protists (Parsons 1966a,b). This trophic breadth can be divided into a dominant group of plant-consuming species (most segmented-beaks, virtually all mouthcones, many siphonostylates, some hexastylates), animal-predators generally on other insects (some segmented-beaks, a few mouthcones, some monostylate/distylates, some distylate/tetrastylates) and blood-feeders (a few segmented-beaks, buccal-cones, hexastylates, tristylates, tubulostylates and probably most siphonostylates). Of the nine mouthpart classes of the series, four are entirely or dominately associated with blood feeding: buccal-cone, hexastylate, tristylate and two others that have blood-feeding as a significant food source: segmented-beaks and siphonostylates. It is noteworthy that whereas the Stylate-Nonhaustellate Series (Section 8.8) is dominated by small, fungal-feeders (Dajoz 1976, Eisenbeis and Wichard 1987, Pakaluk 1987), this dietary grouping is virtually absent in the Stylate-Haustellate Series.

Major Structural Themes. Four major structural themes are present within the Stylate-Haustellate Series (Fig. 28). They are (i) the Mouthcone Class, (ii) the Segmented-Beak and Buccal-Cone Classes, (iii) a dipteran/siphonapteran group consisting of the Monostylate/Distylate, Distylate/Tetrastylate, Hexastylate, Tristylate and Tubulostylate Mouthpart Classes and (iv) the Siphonostylate Mouthpart Class. Each theme is characterized by discrete combinations of characters that resolve stylate-haustellate taxa into these four patterns (Fig. 28).

Mouthcones are the only mouthpart class that is characterized by major mouthpart asymmetry. Uniquely characterizing the class is absence of the right mandible and conspicuous development of both the maxillary and labial palps. The formation of a funnelform mouthcone has parallels in the Buccal-Cone Mouthcone Class, although a similar or analagous structure does not occur in any other stylate-haustellate group.

A second theme consists of segmented-beak and buccal-cone mouthparts that are characterized by the presence of a labially-derived, hemipteroid haustellum devoid of maxillary and labial palps and absence of other labial processes. Segmented-beak and buccal-cone mouthparts are symmetrical, unlike the major mouthpart asymmetry of mouthcone mouthparts, and are opisthorrhynchous rather than the hypognathous or rarely prognathous condition of mouthpart classes of various dipterans, siphonapterans and lepidopterans. Stylet number is four in segmented-beaks and two in buccal-cones.

Five mouthpart classes consisting of dipteran and siphonapteran taxa comprise the third theme of stylate-haustellates. Although similar to the hemipteroids of the second theme in that the haustellum is derived from labial elements (probably labial palps), the third theme has retained maxillary palps and frequently the labial glossa. Stylet number and type is highly variable, unlike other stylate-haustellate themes. Whereas mouthcones bear three stylets and segmented-beak and buccal-cone mouthparts possess four or two stylets, respectively, and siphonostylates one stylet, the five mouthpart classes of the third theme bear one, two, three, four or six stylets. The three-stylate and six-stylate conditions are plesiomorphous for the Siphonaptera and Diptera, respectively, and the three other stylet conditions represent various apomorphic dipteran reduction series.

The fourth theme, the siphonostylate mouthpart class, consists of a single stylet and is a unique modification of the siphonate proboscis (Section 8.6.2) into a piercing organ. Siphonostylates possess virtually all other elements of a lepidopteran facies and are readily differentiated from the hemipteroid and dipteran/siphonapteran groups. Expectedly, siphonostylates clustered with the large siphonate mouthpart cluster (Fig. 28).

Geochronologic Range. Stylate-haustellate mouthparts and the piercing-and-sucking mode of feeding extends to the Late Paleozoic (Carpenter 1971, Kukalová-Peck 1985). During this time, four orders of palaeodictyopteroid insects (Palaeodictyoptera, Megasecoptera, Diaphanopterodea and Permothemistida) constituted the only members of this structural class (Kukalová-Peck 1983) prior to the appearance of homopterans during the Early Permian. These forms apparently consumed a diversity of plant (Carpenter 1971, Sharov 1973) and possibly animal tissue. The types of beaks borne by palaeodictyopteroids ranged from long, slender structures 3.2cm long in adults (Müller 1978) to short, truncate structures about 0.4cm long in nymphs (Labandeira, pers. obs.). Although these taxa were not considered in this analysis, they do exhibit anecdotally a wide diversity of stylate-haustellate beaks present in the Paleozoic insect fauna (Kukalová-Peck, unpubl. MS; Jarzembowski 1987). During the Permian palaeodictyopteroids were replaced by various, modern-aspect hemipteroids and apparently palaeodictyopteroids did not survive into the Mesozoic (Carpenter and Burnham 1985).

The stylate-haustellate component of the modern (i.e. Mesozoic + Cenozoic) insect fauna is documented from the Lower Permian (Rohdendorf and Rasnitsyn 1980) and during the Early Mesozoic surpassed the long-extinct palaeodictyopteroids in ordinal and familial diversity (Sepkoski and Hulver 1985). Segmented-beak homopterans and mouthcone thysanopterans diversified during the Permian (Bekker-Migdisova 1960, 1985; Vishniakova 1981) and later segmented beak heteropterans experienced a radiation during the Early Mesozoic in the freshwater realm (Popov 1971, Andersen 1982). Dipterans began their radiation during the Late Triassic and by the Middle Jurassic added at least three additional stylate-haustellate mouthpart classes (monostylate/distylates, distylates/tetrastylates, hexastylates) to the pre-existing mouthcones and segmented-beaks (after Rohdendorf 1974, Kalugina and Kovalev 1985). These two events--a late Paleozoic/early Mesozoic radiation of hemipteroids and an Early to Middle Mesozoic radiation of dipterans--resulted in the overwhelming bulk of stylate-haustellate taxonomic diversity. Environments into which hemipteroids radiated were several plant-feeding niches during the Permian, including sap-sucking of deep vascular tissue, penetration of shallow nonvascular tissue and punch-and-sucking of pollen and spore grains (from Cobben 1978, Vishniakova 1981). Dipterans and heteropterans subsequently became stylate-haustellate predators on other insects and blood-suckers on vertebrates during the Middle Mesozoic (Downes 1971, Grogan and Szadziewski 1988). Other stylate-haustellate dipteran lineages pierced plant tissues and became attracted to nectar and other sugar-rich plant exudates such as honeydew and resin.

The timing of origin and diversification of the less speciose mouthpart classes--buccal-cone, tristylate, tubulostylate and siphonostylate--is less constrained due to the poor fossil records that are typical of ectoparasitic groups. Analyses of phylogenies of associated hosts often indicate a relatively recent diversification for these mouthpart classes, although the occurrence of Lower Cretaceous tristylates (Jell and Duncan 1986) should introduce a note of caution to the purported recency of these mouthpart classes.

8.9.2. Segmented-Beak Class
(Class 24)

Description. Head shape variable; proboscis (beak) long or very long. Genal region well to moderately developed, rarely absent; gula either prominent and well-developed, or absent; lorum well-developed, less commonly absent. Grasping, raptorial prothoracic legs in some forms. Antennae setaceous or filiform, rarely aristate or serrate; ocelli two, less commonly absent; compound eyes large, expansive or less often moderately developed, rarely absent. Strong, bulbous cylpeal pump present. Mouthparts opisthognathous (sternorrhynchous or auchenorrhynchous), stylate-haustellate with 4 stylets, generally protractile.

Clypeal region prominent and inflated, quadrate to vertically elongate, generally subdivided. Labrum undivided, shape highly variable, a stylet/beak brace. Hypopharynx a salivary syringe with a piston pump, rarely absent; epipharynx a fimbriate or lingulate lobe, acuminately-tapering, rarely with superlingulae. Mandibles acondylic; stylate; serrate, barbate or edentate; generally with a muscle-based lever system for protraction and retraction. Maxilla with a single stipes/cardo sclerite forming the maxillary plate of the "cheek"; palpi and galeae absent. Lacinia stylate, a single blade. Labium extremely reduced; palpi, glossae and paraglossae evidently absent. Labium a 1- to 4-segmented haustellum (=beak) ensheathing mandibular and lacinial stylets. Interregional co-optation of mouthpart elements present.

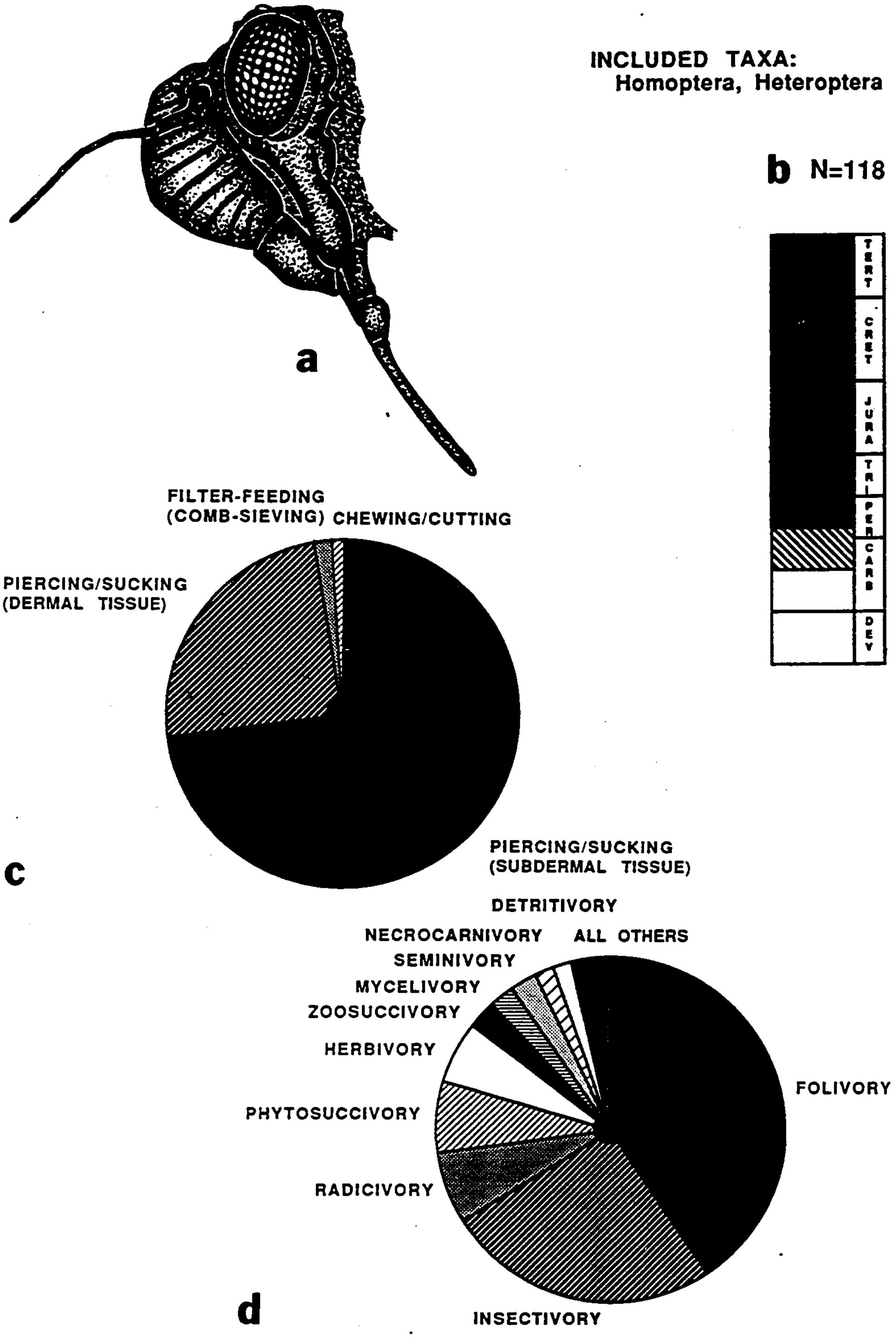
Key Phenocharacters. The segmented-beak mouthpart class is a discrete, highly stereotyped mouthpart class that can not be mistaken for any other mouthpart type. Diagnostic features of the segmented-beak condition are the conspicuous absence of maxillary and labial palps and all endite lobes (galeae, glossae, paraglossae) except the laciniae, which are not externally visible and are prolonged into long, acuminate stylets. The mandibles, like the laciniae, are long stylets and both pairs of stylets are engaged by a muscle-based lever system that protracts and retracts each stylet pair for tissue penetration and withdrawal. The mandibular and lacinial stylets are enveloped by the only evident labial structure: a characteristic, segmented haustellum. (The homologies of the labial haustellum have been much discussed and may represent fused labial palps, or a prolonged and subsegmented ligular structure, or some other labial structure.) The hypopharynx, unlike other stylate-haustellate groups, is not stylate and is a salivary pump. Other characteristic features of segmented-beak mouthparts include a strong, bulging clypeal pump, often with external traces of dilator muscle insertions, and presence of usually prominent lora and maxillary plates in the genal region.

Other stylate-haustellate groups that possibly can be confused with the segmented-beak mouthpart class are mouthcones and tristylates (Sections 8.9.4 and 8.9.8). Mouthcones uniquely possess major head and mouthpart asymmetry and bear three stylets: a short, stouter mandibular stylet and a pair of gracile, but short, bladelike lacinial stylets. The basal maxillary sclerites, labium and labrum form the characteristic funnelform mouthcone that is used as a stylet guide. Tristylates lack mandibular stylets, possessing an epipharyngeal and lacinial stylets which are ensheathed. They feed by protraction of the lacinial stylets by engagement of a lever-based system of segmented, modified labial palps that are individually separate. Tristylates are vertebrate ectoparasites and, unlike segmented-beak members, have spathulate antennae, reduction of compound eyes and absence of ocelli. Other various stylate-haustellate mouthpart classes possess a dipteran head facies and instead of opisthognathous placement of mouthparts on the head, have hypognathous or prognathous placement.

Diversity and Natural History. The Segmented Beak Mouthpart Class is one of the several most abundant mouthpart types occupying terrestrial, freshwater and even marine habitats. It comprises the orders Homoptera and Heteroptera although many coccoid homopterans possess abbreviated mouthparts of the Reduced Trophic Mouthpart Class (Section 8.10.2). The segmented-beak class comprises 110 families, 8960 genera and about 77,000 species (Appendix D) and is five in rank-order of 34 mouthpart classes (Table 5, Fig. 131); it is overwhelmingly the most species diverse mouthpart class that obtains food by piercing-and-sucking. Members of this structural group are probably monophyletic and there is no indication of structural convergence. The Segmented Beak Mouthpart Class is a relatively old group; the earliest known fossils occur in Lower Permian deposits (Bekker-Migdisova 1940, 1960). However, four orders of unrelated (Crampton 1927, Kukalovä-Peck 1983) Late Carboniferous to Late Permian palaeodictyopteroids had analogous mouthparts and if these fossil species were included in the data-set, they probably would have clustered as a separate but closely associated group. (This possibility is indicated in Fig. 133, column 24).

Segmented-beaks are the major participants responsible for consuming unexposed, intracellular and intercellular fluid of plants, particularly the sap of vascular tissues such as xylem, phloem and tracheids (Risebrow and Dixon 1987). They are also important fluid feeders on other insects and vertebrate blood (see Smith [1985] for a review of feeding mechanisms) although other stylate-haustellate classes are also important fluid-feeding insectivores and sanguinivores. (Fig. 98 illustrates the dietary breadth of segmented-beak members.)

Although virtually all members of this mouthpart class belong to the piercing-and-sucking functional-feeding-group, some aphids are plant-gallers (Southwood 1973, Forrest 1987) and several corixid genera are filter-feeders even though they have stylate, albeit truncate and abbreviated mouthparts (Benwitz 1956; Parsons 1966a,b). Most of the dietary data is for agriculturally-important herbivores, particularly aphids, whiteflys and scale insects, although a few heteropterans, such as the milkweed bug, *Oncopeltis fasciatus* (Dallas) and certain pathogen-transmitting, sanguinivorous cimicids and reduviids also have been



INCLUDED TAXA:
Homoptera, Heteroptera

FIGURE 98. Overview of the Segmented Beak Mouthpart Class. a, *Magicicada septendecem* (Linneaus) (Homoptera: Cicadidae, data-set no. 317), after Snodgrass (1921); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

extensively investigated. Plant-feeding members of the Segmented-Beak Class include all homopterans and many heteropterans; animal-feeding members are principally insectivorous and include the terrestrial heteropteran families Nabidae and Anthocoridae in addition to about 15 aquatic families in the suborders Nepomorpha and Gerromorpha (Cobben 1978). Obligate sanguinivores include the human-infesting Reduviidae and Cimicidae and the bat ectoparasite Polyctenidae (Hagen 1987). The transfer to vertebrate sanguinivory probably evolved from fluid-feeding insectivory (Brues 1972).

Within the plant-feeding group there is a variety of diets, host-specificities and mouthpart-related adaptations for extracting liquid nutriment from subsurface tissue. All plant organs, including roots, leaves, stems and various reproductive structures, are attacked. Many species, such as coccoids (Risebrow and Dixon 1987) are restricted to particular host species, whereas others, such as cicadas, are less restricted and may feed on roots as nymphs and twigs and leaves as adults (Brues 1972). For both host-specific and host-nonspecific members there is frequently a subdivision of plant tissue use, with forms with long beaks piercing deep vascular tissue and those with short beaks feeding on leaf epidermis or mesophyll (Carter 1962); other studies (e.g. Hajek and Dahlsten 1986) have concluded that leaf phenological state is important in this context.

Host specificity is probably best demonstrated in the phloem-feeding guild which comprises homopterans belonging to the Psylloidea, Aleyroiidea, Aphidoidea and Coccoidea. These four groups feed by inserting stylets deep into vascular tissue and line the puncture with a mucilaginous, hardened sheath that allows for stylet movement (Barbosa and Wagner 1989). Forms without a stylet sheath are not phloem feeders and simply puncture individual cells or intercellular material directly. Host psyllids and aleyrodids are often polyphagous on woody plants whereas most coccoids (scale insects) are monophagous on woody plants. Within the Aphidoidea, most exhibit host-specificity (Heie 1967, Risebrow and Dixon 1987) and more than 50% are host-specific to a single plant genus (Eastop 1973). All four groups remove vast quantities of sap from the hosts, most of which is secreted a sugary honeydew--a waste byproduct resulting from the simultaneous removal of vast quantities of sap from plant hosts and the retention of low quantities of sap amino acids essential for insect nutrition (Mitter 1958). This honeydew in turn is consumed by ants as food (Schowalter et al. 1988; Section 8.3.6) and the aphids are accordingly protected from predators since their honeydew is a valuable food sources for ants. Because of the low levels of amino acids in plant saps, most phloem-feeders feed virtually continuously and extraction rates of amino acids range from 55% or more (Mitter 1958). Phloem-feeders can introduce viruses and toxic saliva chemicals into plant vascular systems (Risebrow and Dixon 1987) and plants are known to secrete sap allelochemicals (Wink et al. 1982) and exude surface phagodeterrants to deter predation as well.

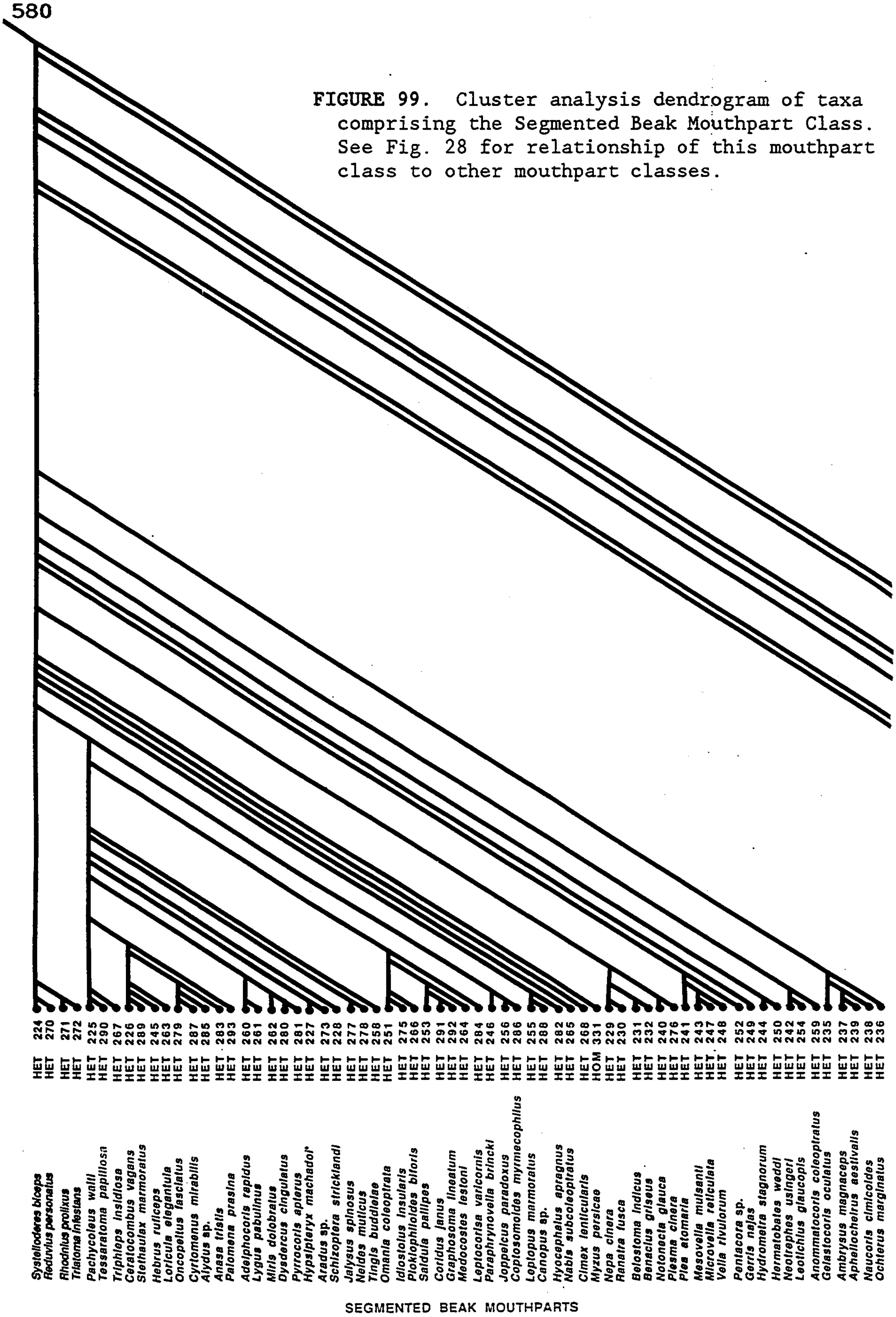
There are two fundamental strategies of extracting amino acids from plant tissues. One is sap-sucking and thus increase sap throughput, as mentioned above for homopterans. The other is to engage in selective feeding, as in heteropterans that consume on seeds, flower buds and shoot meristems (Southwood 1973). An example of the second strategy are seed bugs that include members of the Coreidae, Lygaeidae, Miridae, Pentatomidae, Pyrrhocoridae and a few other less diverse families (Slansky and Panizzi 1987). Seeds contain from 2 to 60% protein (dry weight) and from 1 to over 70% oil (Jones and Earle 1966), although many seeds contain toxic substances such as glycosides, alkaloids and polyphenols to repel predators (Herrera 1982). Other devices for limiting predation include small seed size and restriction of temporal availabilty. Nevertheless seed predation is a nutritionally profitable enterprise: seed-suckers typically inject watery saliva with digestive enzymes after puncturing endosperm and suck out the liquified slurry in a "lacerate-and-flush" technique (Goodchild 1966).

Segmented-beak heteropterans have radiated several times into various predatory niches in freshwater and to a lesser extent, marine ecosystems (Cobben 1978, Andersen 1982). These dominately insectivorous and small vertebrate predating forms have invaded the water surface, neuston, benthic and nektonic zones of water bodies. For example, nektonic belostomatids (predaceous diving bugs) are up to 11cm long and prey on other insects, small fish and tadpoles, whereas gerrids (pond skaters) feed on insects on the water surface (Sih 1987), and notonectids (backswimmers) feed on small insects among subaquatic plants (Richards and Davies 1977).

The plant-feeding, piercing-and-sucking functional-feeding-group, which is dominated by segmented-beaks, is an important component of plant consumers in virtually all ecosystems. Moran and Southwood (1982) determined that the sap-sucking guild was a major component of the arthropod fauna from British and South African trees. Stork (1987) arrived at the same conclusion and demonstrated that the proportional composition of the sap-sucking guild was not appreciably different between English cool-temperate forest and Bornean rainforest. In various plant groups inventories of the proportional distribution of various feeding guilds have shown that sap-suckers are an important component. This importance has been documented for *Cryptomeria* (Taxodiaceae) trees in Japan (Hijii 1986), thistles (Asteraceae) in southern California (Goeden and Ricker 1987b) and for *Baccharis* (Asteraceae) shrubs in Texas, Louisiana and northern Mexico (Palmer 1987). Lastly, in addition to ingesting fluid food, segmented-beak members are known to be incidental pollinators (Porsch 1957, Kevan and Baker 1984).

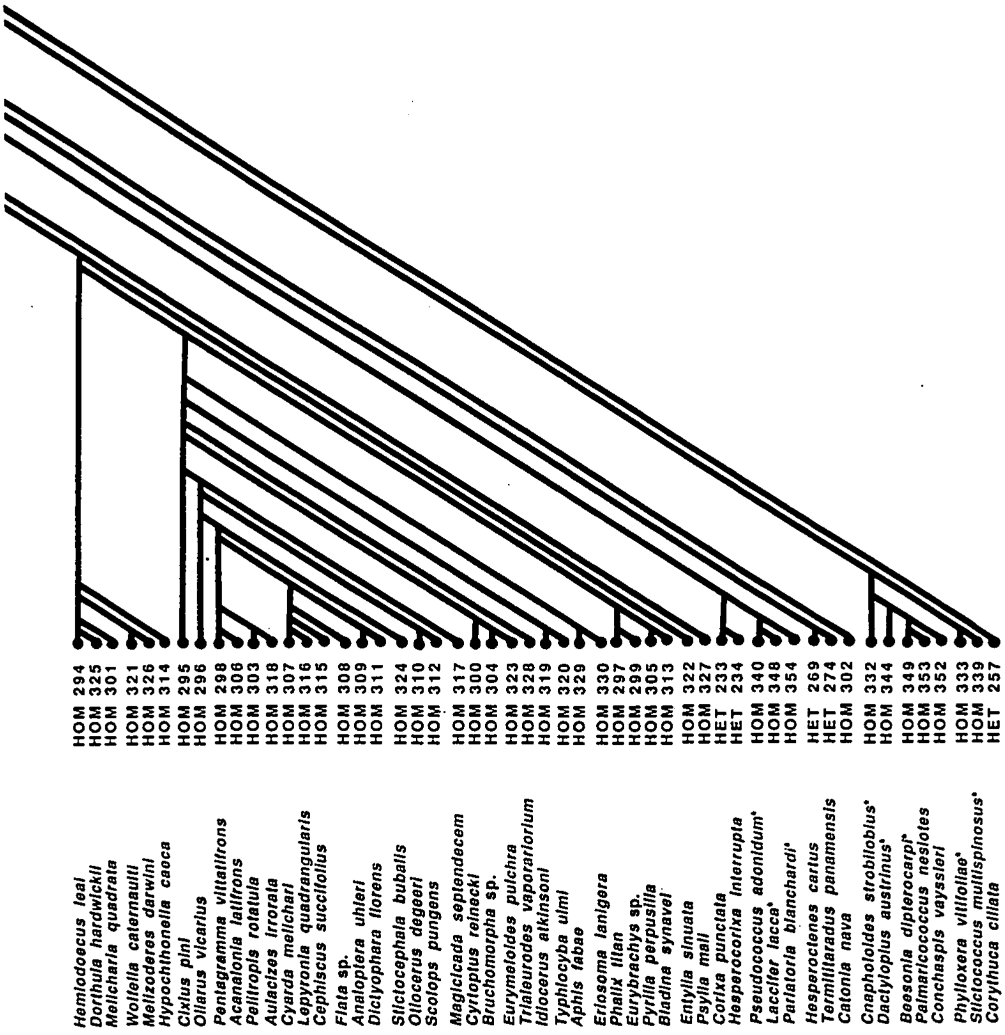
Structural Themes. Two fundamental structural themes are clearly defined within the Segmented Beak Mouthpart Class. The first theme is Subcluster 1 (data-set entries 224 to 236 of Fig. 99) which contains 98.5% heteropterans, whereas the second theme (Subcluster 2, 291 to 257) is characterized by a 90% dominance of homopteran taxa. The differences between these two subclusters are minor and involve consistently only five characters. Some important subthemes occur in both subclusters.

The first theme notably comprises taxa whose opisthognathous mouthparts are placed sternorrhynchously on the head--that is, the mouthparts are held under the venter of the head and thorax. Other features include the presence and frequent prominence of a gula, filiform antennae, an epipharynx with a prelabral gutter and sensory organ forming the ventral part of the food pump and mandibular stylets that tend to be barbate or serrated. The most interesting subtheme is



HET 224 Systelloderes biceps
HET 270 Reduvius personatus
HET 271 Rhodnius prolixus
HET 272 Triatoma infestans
HET 225 Pachycoleus waltli
HET 290 Tessaratoma papillosa
HET 267 Triphleps insidiosa
HET 226 Ceratocombus vagans
HET 289 Stethaulax marmoratus
HET 245 Hebrus ruficeps
HET 263 Loricula elegantula
HET 279 Oncopeltus fasciatus
HET 287 Cyrtomenus mirabilis
HET 285 Alydus sp.
HET 283 Anasa tristis
HET 293 Palomena prasina
HET 260 Adelphocoris rapidus
HET 261 Lygus pabulinus
HET 262 Miris dolobratus
HET 280 Dysdercus cingulatus
HET 281 Pyrrocoris apterus
HET 227 Hypsipteryx machadoi*
HET 273 Aradus sp.
HET 228 Schizoptera stricklandi
HET 277 Jalysus spinosus
HET 278 Neides muticus
HET 258 Tingis buddleiae
HET 251 Omania coleoptrata
HET 275 Idiostolus insularis
HET 266 Plokiophiloides biloris
HET 253 Saldula pallipes
HET 291 Coridus janus
HET 292 Graphosoma lineatum
HET 264 Medocostes lestoni
HET 284 Leptocorisa varicornis
HET 246 Paraphrynovelia brincki
HET 256 Joppeicus paradoxus
HET 286 Coptosomoides myrmecophilus
HET 255 Leptopus marmoratus
HET 288 Canopus sp.
HET 282 Hyocephalus apragnus
HET 265 Nabis subcoleoptratus
HET 268 Cimex lenticularis
HOM 331 Myzus persicae
HET 229 Nepa cinera
HET 230 Ranatra fusca
HET 231 Belostoma indicus
HET 232 Benacus griseus
HET 240 Notonecta glauca
HET 276 Plesma cinera
HET 241 Plea atomaria
HET 243 Mesovelia mulsanti
HET 247 Microvelia reticulata
HET 248 Velia rivulorum
HET 252 Pentacora sp.
HET 249 Gerris najas
HET 244 Hydrometra stagnorum
HET 250 Hermatobates weddi
HET 242 Neotrephes usingeri
HET 254 Leotichius glaucopis
HET 259 Anommatocoris coleoptratus
HET 235 Gelastocoris oculatus
HET 237 Ambrysus magnaceps
HET 239 Aphelocheirus aestivalis
HET 238 Naucoris cimicoides
HET 236 Ochterus marginatus
SEGMENTED BEAK MOUTHPARTS

FIGURE 99. Cluster analysis dendrogram of taxa comprising the Segmented Beak Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.


Hemiodoecus leai HOM 294
Dorthula hardwickii HOM 325
Melicharia quadrata HOM 301
Woitella caternaulti HOM 321
Melizoderes darwini HOM 326
Hypochthonella caeca HOM 314
Cixius pini HOM 295
Oliarus vicarius HOM 296
Pentagramma vittatifrons HOM 298
Acanalonia latifrons HOM 306
Pelitropis rotulata HOM 303
Aulacizes irrorata HOM 318
Cyarda melichari HOM 307
Lepyronia quadrangularis HOM 316
Cephiscus succifolius HOM 315
Flata sp. HOM 308
Anaioptera uhleri HOM 309
Dictyophara florens HOM 311
Stictocephala bubalis HOM 324
Otiocerus degeeri HOM 310
Scolops pungens HOM 312
Magicicada septendecem HOM 317
Cyrtopius reinecki HOM 300
Bruchomorpha sp. HOM 304
Eurymeloides pulchra HOM 323
Trialeurodes vaporariorum HOM 328
Idiocerus atkinsoni HOM 319
Typhlocyba ulmi HOM 320
Aphis fabae HOM 329
Eriosoma lanigera HOM 330
Phalix titan HOM 297
Eurybrachys sp. HOM 299
Pyrilla perpusilla HOM 305
Bladina synavei HOM 313
Entylia sinuata HOM 322
Psylla mali HOM 327
Corixa punctata HET 233
Hesperocorixa interrupta HET 234
Pseudococcus adonidum* HOM 340
Laccifer lacca* HOM 348
Parlatoria blanchardi* HOM 354
Hesperoctenes cartus HET 269
Termitaradus panamensis HET 274
Catonia nava HOM 302
Cnapholoides strobilobius* HOM 332
Dactylopius austrinus* HOM 344
Beesonia dipterocarpi* HOM 349
Palmaricoccus nesiotes HOM 353
Conchaspis vayssieri HOM 352
Phylloxera vitifoliae* HOM 333
Stictococcus multispinosus* HOM 339
Corythuca ciliata HET 257

SEGMENTED BEAK MOUTHPARTS

isolation of various sanguinivorous forms, including reduviids (taxa 270 to 272) and the bedbug *Cimex lectularis* Linneaus (268) into separate subclusters.

By contrast the second theme consists of homopteran taxa whose mouthparts characteristically are auchenorrhynchously attached to the head, projecting below the neck. Other distinguishing characters include the absence of a gula, setaceous antennae, a membranous epipharynx and mandibles that tend to be edentate and serrated. Interesting subclustering patterns involve the presence in the homopteran dominated subclusters of the only filter-feeding forms, the heteropterans *Corixa punctata* (Illiger) (233) and *Hesperocorixa interrupta* (Say) (234). These taxa have a modification of the beak into a stout, funnelform, filter-feeding organ (Benwitz 1956). Also, the blind, parasitic to semiparasitic heteropterans *Hesperoctenes cartus* Jordan (269) and *Termitiaradus panamensis* Myers (274) form a separate subcluster, as does the somewhat distinctive *Corythuca ciliata* Say (257) of unknown habits. These heteropteran taxa are atypical structurally and ecologically when compared to those heteropterans occurring in the subcluster of the first theme.

Geochronologic History. Two major features of the geochronologic history of the segmented-beak mouthpart class are discussed in this section. First is the historical record provided by fossils. Second are various ideas and data from the biogeography and phylogeny of Recent clades of segmented-beaks and their angiosperm plant hosts for the timing of various coevolutionary relationships. From the fossil record and phylogenetic relationships of the segmented-beak mouthpart class shown in Fig. 100, two major diversification events are evident. An earlier event during the Late Carboniferous to Early Permian represents the radiation of several plant-feeding homopterans (Popov 1980, Bekker-Migdisova 1985). In uppermost Carboniferous deposits of the Kusnetsk Basin in central Asia [97] and Lower Permian deposits [89] of the USSR the most plesiomorphic homopteran clade, the Archescytinomorpha, are first recorded (Bekker-Migdisova 1960). Also in the same Kusnetsk deposits occur species of the slightly less plesiomorphic Prosobolomorpha (Bekker-Migdisova 1960). From the Late Permian of the USSR [87], the cixiid fulgoroidean *Scytocixius mendax* Martynov 1937 signals the earliest occurrence of the extant clade, Cicadomorpha. A fulgoroidean cicadomorphan, *Mundus nodosus* Bekker-Migdisova 1960 is also known from penecontemporaneous deposits in the USSR [86], as is the earliest known psyllomorph, *Permaphidopsis sojanensis* Bekker-Migdisova 1960, although Wootton and Popov (1977) consider this latter taxon an archescytinomorphan. If Bekker-Migdisova's identification is correct, the existence of the sister-group to the Psyllidae, the Aleyrodidae (whiteflies) also occurred during the Late Permian.

Although *Kaltanaphis permiensis* Bekker-Migdisova 1959 from the lower Upper Permian of the Kusnetsk Basin [97] was once considered an early aphid, it lacks the basic synapomorphies of the group (Szelegiewicz and Popov 1978, Hennig 1981); it is probably an archescytinomorphan. The earliest assured aphid is *Penaphis circa* Lin 1980 from the Middle Jurassic of China [64] (Jarzembowski 1989) and the earliest occurrence of the sister-group to the Aphidoidea, the Coccoidea (scale insects), may be *Mesococcus asiaticus* Bekker-Migdisova from the Triassic/Jurassic boundary of the USSR [73], although the earliest convincing coccoid is significantly younger. The extinct Progonocimicimorpha, in many ways is structurally transitional between the Homoptera and Heteroptera (Popov and Wootton 1977), originated during the Early Permian and existed until the Late Cretaceous[46] (Kormilev and Popov 1986).

The second or later event was the radiation of aquatic and terrestrial heteropterans during the later Triassic (Fig. 100). Although both aquatic predaceous and terrestrial herbivorous taxa appear early during this diversification, the aquatic infraorders comprise forms that can be placed in modern families whereas the terrestrial infraorders represent extinct families (Whalley 1985). For the plesiomorphous aquatic infraorder Enicocephalomorpha the earliest representative is *Cuneocoris geinitzi* Handlirsch 1908 (Popov and Wootton 1977) from the Lower Jurassic of Germany [68] (Popov and Wootton 1977). Its sister-group, the aquatic and predatory Gerromorpha enters the known fossil record in the Late Triassic of Virginia [76]. Nepomorphans, including some of the largest aquatic insects known, first occur in the slightly younger Upper Triassic of Australia [74] and includes the triassocorid *Triassocoris myersi* Tillyard 1923. Later-occurring gerromorphans include the belostomatid (giant water bug) *Mesonepa* (Whalley 1985) from the Lower Jurassic of England [69] and the corixid (water boatman) *Yanliaocorixa chinensis* Lin (Hong 1983) from the Middle Jurassic of China [64]. The

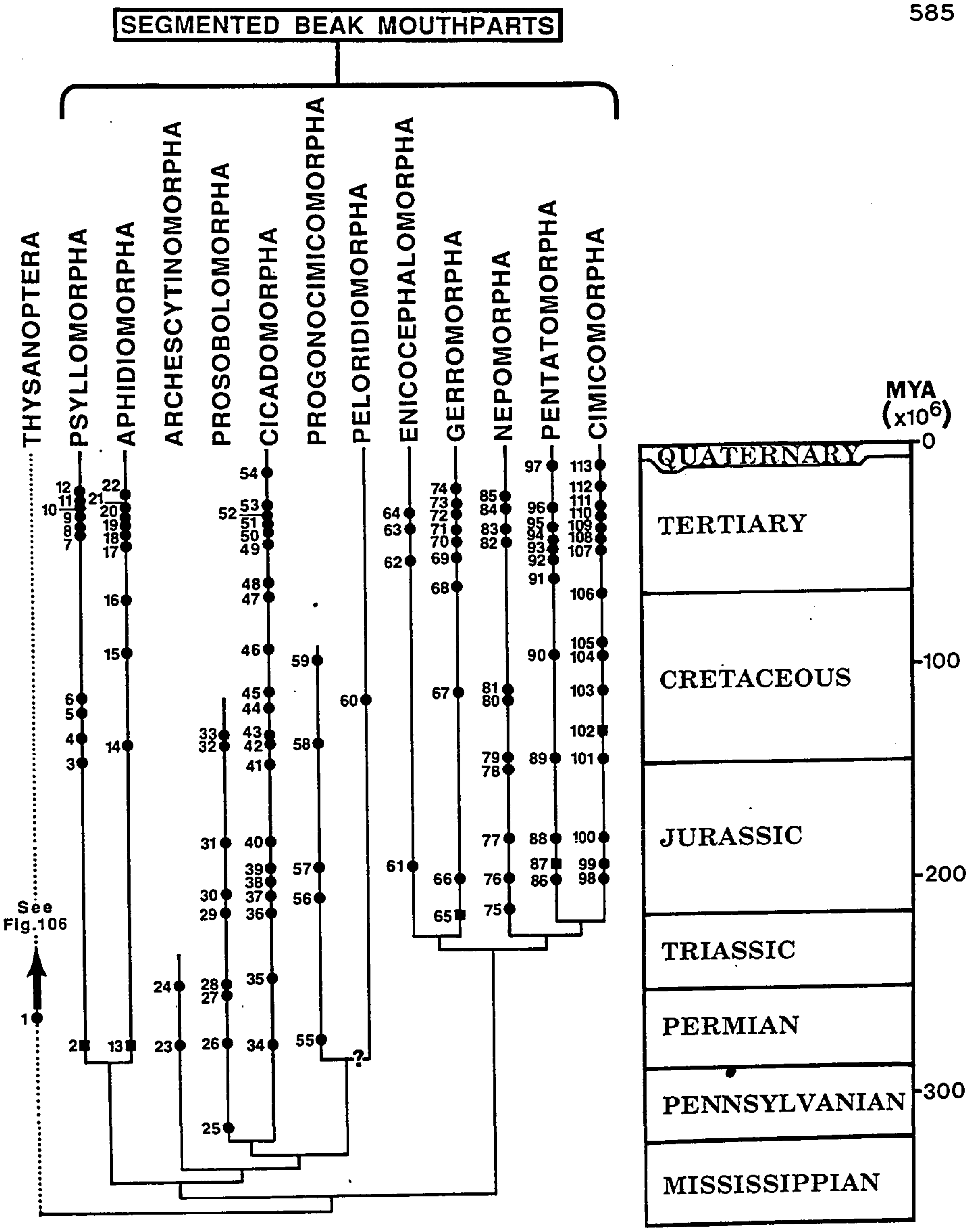


FIGURE 100. Geochronologic history of the Segmented Beak Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Rieger (1976), Popov (1980), Kristensen (1981) and Strümpel 1983. The taxonomic level of analysis is the infraorder. The outgroup is Thysanoptera. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.

remaining infraorder, the terrestrial Cimicimorpha, first occurs in the same Chinese deposit (Hong 1983) and its constituent Miridae (plant bugs), Anthocoridae (minute pirate bugs) and Microphysidae are known from later Jurassic and Cretaceous deposits [60,53,37] (Popov 1968, Jell and Duncan 1986, Zherikin and Sukacheva 1973, respectively). The enigmatic, freshwater-inhabiting, gerrid-like Chresmodidae from Middle Mesozoic deposits has been considered variously as phasmids (Martynov 1928), a surviving member of the Late Paleozoic/Triassic Paraplecoptera (Martínez-Delclós 1989) and heteropterans on water surfaces (Popov 1980), although Baudoin (1980) demonstrated that one species was too large to be supported by surface water tension. Popov (1971), Cobben (1978) and Andersen (1982) have provided monographic accounts of various aspects of this heteropteran radiation.

Although all homopterans are essentially herbivorous, heteropterans are both herbivorous and insectivorous. This fact and a detailed analysis of mouthpart structures led Cobben (1978) to pose a primarily insectivorous and hydrophilous life-habit as ancestral for heteropterans (see also Southwood 1973). Sweet (1979) presented contrary evidence and marshalled paleontological, morphological, ecological and phylogenetic evidence to indicate that heteropterans were primitively herbivorous like their sister-group, the Homoptera. While the debate continues, there is widespread agreement that the ancestral homopteran was a sap-sucking herbivore (Heie 1967, Popov 1980, but see Goodchild 1966), a conclusion that led Downes and Dahlem (1987) to propose that homopteran, sugar-rich honeydew was the original food resource for labellate adult dipterans during the preangiospermous Mesozoic. Thus the fleshy, sponging, pseudotracheate labellum of dipterans (see Section 8.5.3) was exapted to later sequester nectar as a food source when anthophily became dominant. This general theme was re-expressed by Grinfel'd (1961) who postulated that aphid honeydew was a major food source in the development of ants (see Section 8.3.6).

There is considerable evidence that many homopteran/vascular plant associations are pre-Gondwanan (Early Mesozoic) in origin, conservative in evolutionary mode and only gradually accomodating to host shifts, with wholesale host shifts on taxonomically-unrelated hosts rare. Examples of this phenomenon include psyllids (Hodkinson 1985, 1989) and aphids (Eastop 1973). Additional supportive evidence is recent documentation by Moran (1989) of coevolutionary constancy in an aphid/moss/sumac plant partnership for the past 48 million years. These observations are seemingly at odds with a recent evaluation of whether herbivory has promoted demonstrable diversification in insect clades with nonherbivorous sister-groups (Mitter et al. 1988). For virtually all groups of examined herbivorous clades among homopterans and heteropterans there was evidence for significantly greater taxonomic diversification in the herbivorous sister-group than in the nonherbivorous sister-group. The solution to these two types of data and contrary conclusions may involve acceptance of homopteran lineages diversifying on particular host taxa, but inferring that the taxonomic *range* of colonized plant taxa has an upper limit and in some cases may constrain ultimately homopteran clade diversity.

Previous Designations. The mouthpart grouping that is herein termed the **segmented-beak** has a long history of being recognized by entomologists (Table 6). Aristotle apparently did not make a reference to it. Within the premodern era Fabricius (1775) referred to a particular insectan group, the Ulonata, as forms possessing a "maxillae covered by a sheath" but considered the possessors of this condition as essentially mandibulate. Fabricius later (1799) refined this designation by considering the same group of insects, renamed "Rhyngota" as bearing sucking mouthparts and possessing "for the mouth a chitinous, jointed, hinged proboscis," which were contrasted to different mouthpart structures in the Glossata (=Lepidoptera) and Antliata (=Diptera). MacLeay (1821) subsequently divided insects into two series, the Mandibulata and the Haustellata, and ordinated these series into five developmentally-based groups. His fourth category was "metamorphosis half-complete; larvae similar to adult" in which he considered the mandibulate version as "Orthoptera" (undoubtedly *sensu lato*) and the haustellate version as "Hemiptera." In a standard textbook, Kirby and Spence (1826) devised a key for insects which dichotomized forms into those with mandibulate mouthparts and those with haustellate mouthparts. The Hemiptera was considered a haustellate group. Finally, the noted French entomologist, Latreille (1832) considered hemipterans as the only group of "elytropterous" insects with sucking mouthparts.

Recently, what is herein considered as the Segmented Beak Mouthpart Class has been referred to in functional and taxonomic terms as the "hemipterous subtype" of the "piercing-and-sucking" type by Metcalf

(1929) and Metcalf et al. (1962), and the "hemipteran type" of the piercing-sucking group by James and Harwood (1969) (Table 6). Previous terms designating this mouthpart type have focused on the taxonomic description "hemipteran" or the functional term "piercing-and-sucking." These terms do not refer to the structurally most important feature of the mouthpart type: the segmented-beak. Additionally, "piercing-and-sucking" can apply to almost half of the mouthpart classes of this study. For these reasons, I am appropriating the term, segmented-beak, as a name for this class. Recent extensive treatments of this mouthpart class are provided by Matsuda (1965), Denis and Bitsch (1973), Cobben (1978) and Smith (1985).

Review of Literature. The mouthpart- and head-related literature of the Segmented Beak Mouthpart Class is voluminous. In the ensuing discussion I will define particular themes within this literature, citing important sources of documentation. Although this review is not comprehensive, hopefully it will provide insight into the types and traditions of research on segmented-beak mouthparts.

Several major monographic accounts of segmented-beak head and mouthpart structure have been published, the most notable which is Cobben's (1978) exhaustive compilation of heteropteran mouthpart (especially stylet) structure in his detailed analysis of feeding mechanisms among the Heteroptera. Earlier, Spooner (1938) extensively documented head, beak and stylet structure for representative genera within most commonly-occurring heteropteran and homopteran families. Kramer (1950) discussed mouthpart structure in his study of auchenorrhynchous homopteran evolution. Barth (1952, 1953) investigated stylet structure, piercing mechanism and mode of feeding in the sanguinivore *Triatoma infestans* (Klug). Subsequently Pollard (1973, 1977) extended these studies to herbivorous forms, presenting reviews explaining the mechanism of plant damage by aphids. More peripheral but important major investigations of head and mouthpart structure include Mordvilko's (1934) neontologically oriented review of aphid evolution, Goodchild's (1966) examination of alimentary canal structure and the evolution of feeding habits in hemipterans, and lastly Miles' (1987) and Klingauf's (1987) discussions on feeding adaptations and feeding behavior in hemipterans, especially aphids and hoppers.

General reviews of the structure and homologies of the hemipteran cranium and its mouthparts are those of Geise (1883), Marlatt (1895), Meek (1903), Bugnion and Popoff (1911) and Muir and Kershaw (1911, 1912). These studies were followed by more detailed examinations that documented the comparative structure and inferred phylogenetic relationships of many more taxa. Examples include Evans (1938), Butt (1943), Parsons (1964), Puchova (1970), Singh (1971) and Hamilton (1981). Many of these studies derived inspiration from Weber's (1928) classic study of the mechanism of hemipteran stylet action and tissue penetration. Specific anatomic regions of the hemipteran cranium and mouthparts have garnered special attention by morphologists and include the maxillary plates (Snodgrass 1938, Evans 1973, Bourgoin 1986), structure and mechanism of the salivary and food pumps (Servadei 1946; Qadri 1951, 1959; Popham 1962; Saxena 1963; Parsons 1963, 1966a,b, 1972 and Rastogi 1965), cephalic glands (Banks 1939, Parsons 1958), labium structue (Parsons 1966c, 1969; Stys 1969; Jarial et al. 1969), stylet ultrastructure and penetration mechanism (Wedde 1885; Forbes 1969, 1972, 1976, 1977; Forbes and Mullick 1970; Forbes and Raine 1973), and documentation of the watchspring-like condition of many exceptionally long stylets that are housed in cephalic capsules (Spooner 1920, China 1931, Cobben 1978).

Studies specifically focusing on head and mouthpart structure of usually economically important species are an important source of data-set documentation. For heteropterans the following taxa have been documented: the nepid *Ranatra fusca* Beauvois by Neiswander (1926); the belostomatids *Belostoma indicus* Le Peletier and Servadei by Verma et al. (1973), and *Benacius griseus* (Say) and *B. uhleri* (Montandon) by Parsons (1966); the corixid *Corixa punctata* Illiger by Benwitz (1956); the gelastocorid *Gelastocoris oculatus* (Fabricius) by Parsons (1959); the ochterid *Ochterus marginatus* Latreille by Rieger (1975); the naucorid *Naucoris cimicoides* Linneaus by Bekker (1929); the gerrid *Gerris remiges* Stal by Wirtz (1987); the pyrrhocorids *Dysdercus cingulatus* Fabricius by Rathore (1961), *D. fasciatus* Signoret by Khan (1972), *D. intermedius* Distant by MacGill (1907) and *D. koenigii* Fabricius by Kumari (1955); and the coreid *Anasa tristis* DeGeer by Tower (1914). For homopterans the following taxa have been described: the cicadids *Magicicada* sp. by Snodgrass (1921) and *Platypleura octoguttata* by Murti (1929); the cicadellids *Idiocerus atkinsoni* Lethierry by Arora and Singh (1962), *I. clypealis* Lethierry by Qadri (1949) and *Typhlocyba ulmi* Linneaus by Willis (1949); the psyllid *Psylla mali* Schmidberger by Grove (1919), Brocher (1925) and Weber (1928); and the aphidid *Eriosoma lanigera* (Hausmann) by Davidson (1914).

Another source of head and mouthpart data originates from taxonomic monographs or shorter works of species- or genus-level systematics or descriptions of taxa for existing or newly-erected families. Heteropteran examples include the following taxa and their documentors: the dipsicorid *Hypsipteryx machadoi* Drake by Stys (1970), the nepid *Nepa cinera* Linneaus by Hamilton (1931), the helotrephid *Neotrephes usingeri* China by China (1935), the paraphrynovelid *Paraphrynovelia brincki* Poisson by Anderson (1978), the gerrid *Gerris najas* DeGeer by Brinckhurst (1960), the gerrid *Hermatobates weddi* China by China (1957), the omaniid *Omania coleoptrata* Cobben by Cobben (1970), the leotichiid *Leotichius glaucopis* Distant by China (1933), the leptopodid *Leptopus marmoratus* Goeze by China (1933), the joppeicid *Joppeicus paradoxus* Puton by China (1955) and Davis and Usinger (1970), the vianaidid *Anommatocoris minutissimus* China by China (1945) and Drake and Davis (1959), the medocostid *Medocostes lestoni* Stys by Stys (1967), the plokiophilid *Plokiophiloides pilosus* Caryon by Caryon (1974), the polyctenid *Hesperoctenes cartus* Jordan by Ferris and Usinger (1939), the termitiaphidid *Termitiaradus panamensis* Myers by Myers (1924), the idiostolid *Idiostolus insularis* Berg by Scudder (1962), the piesmatid *Piesma cinerum* (Say) by Drake and Davis (1958) and the hyocephid *Hyocephalus apragnus* Bergroth by Stys (1964). Homopteran examples include the following taxa and their documentors: the tettigonometrid *Phalix titan* Fennah by Fennah (1952), the eurybrachid *Eurybrachys tomentosa* Fabricius by Chatterjee (1933), the lophopid *Pyrilla* *perpusilla* (Walker) by Qadri and Aziz (1950), the nogodinid *Bladina* sp. by Fennah (1952) and Kramer (1976), the hypochthonellid *Hypochthonella caeca* China and Fennah by China and Fennah (1952), the cicadellid *Idiocerus* sp. by Tribout (1956), the aleyrodid *Trialeurodes vaporariorium* (Westwood) by Hargreaves (1915), the adeligid *Cnaphalodes strobilobius* Kaltenbach by Speyer (1923), the phylloxerid *Phylloxera* sp. by Duncan (1922) and Maillet (1957), the stictococcid *Stictococcus multispinosis* Newstead by Richard (1971), the pseudococcid *Pseudococcus* sp. by Makel (1942), Jancke (1955) and Giliomee (1961), the dactylopiid *Dactylopius austrinus* DeLotto by DeLotto (1974), the kerrid *Laccifer lacca* Kerr by Stebbing (1910) and Imms and Chatterjee (1915), the besoniid *Beesonia dipterocarpi* Green by Green (1926), the conchaspidid *Conchaspis vayssieri* Mamet by Mamet (1954) and the phoenicococcid *Palmaricoccus nesiotes* (Laing) by Zimmerman (1948). Many of these data sources are descriptions of newly discovered species that became the basis for the establishment of new families. Often such sources were the only data for head- and mouthpart-related features for these species.

Finally, other studies of segmented-beak mouthparts have delved into the mechanism of stylet penetration of plant (particularly phloem) tissues and vertebrate capillaries. Observational data on homopteran penetration of phloem and xylem tissues include Mitter et al. (1957, 1958) for uptake of *Salix* (willow) phloem sap by the aphid *Tuberolachnus salignus* (Gmelin), Pollard (1959) for the tissue preferences of the tingid *Urentius aegypticus* Bergevin on *Solanum* (eggplant), McAllan and Adams (1961) for use of pectinase by aphids in the penetration of plant tissue, Evert et al. (1968) for stylet penetration of *Tilia* (linden) branches by the aphid *Longistigma caryae* (Harrison), Tedders and Thompson (1981) on an histological investigation of feeding damage to *Prunus* (peach) foliage by three aphid species, Kimmins and Tjallingii (1985) who examined sieve element penetration by aphid stylets (see Peel [1975] for a review) and Walker (1985) who measured the effect of leaf age on stylet penetration by the aleyrodid *Parabemisa myricae* (Kuwana). Bornman and Botha (1973) and Dixon (1975) have provided reviews of the nutritional ecology and feeding of aphids on phloem. The heteropteran counterpart of phloem-stylet research is more limited but involves studies of stylet penetration of blood capillaries by various sanguinivores, particularly *Triatoma infestans* (Klug) and *Cimex lectularis* Linneaus (Dickerson and Lavoipierre 1959, Lavoipierre et al. 1959, Bernard 1974 and Haridass 1985). Exquisite scanning electron micrographs of heads and stylets are provided by Cobben (1978) and Eisenbeis and Wichard (1987).

8.9.3. Buccal-Cone Class
(Class 25)

Description. Head quadrate to porrect; proboscis short to occasionally long. Genae absent; gula prominent. Antennae filiform, rarely serrate; ocelli absent; compound eyes absent, rarely present. Mouthparts prognathous, protractile, stylate-haustellate (rarely nonhaustellate?), with two (rarely one) stylets. Food pump cibarial, clypeal, or both.

Clypeus quadrate, infrequently otherwise. Labrum variously shaped, undivided, with an apertuate or notched apex, forming a stylet-guide. Hypopharynx long and stylate, with a salivary syringe; epipharynx membranous. Mandibles monocondylic; dimunitive; excavate; edentate; characterized by musculation of protraction/retraction. Maxillae with stipes equant or elongated, apalpate, bearing a tubulate, amplexiform galeae only. Labium with basal region transversely elongate, apalpate and bearing a ligulate stylet. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. The most distinctive attribute of the buccal-cone mouthpart class is the unique arrangement of the two mouthpart stylets that originate from unpaired mouthpart elements. These are the hypopharyngeal "dorsal stabber" and the labial "ventral stabber"--an association that is not found in any other mouthpart class. Most buccal-cone mouthparts are extremely reduced or absent; maxillary and labial palps are absent and apparently there has been incorporation of mandibular sclerites (the mandible itself?) into the buccal-cone wall. Further reductions, indicative of an ectoparasitic life-habit are the absence of ocelli and the frequent absence of compound eyes. (When compound eyes are present, they are significantly reduced.)

The buccal-cone mouthpart class is probably most similar to the mouthcone mouthpart class discussed in Section 8.9.4. Substantive differences between the two include the unique hypopharyngeal and labial stylet arrangement, palpal absence, and absence of functioning mandibles among buccal-cone mouthparts, as well as the prognathous placement of buccal-cone mouthparts compared to the opisthognathous placement of mouthcone mouthparts. Although the segmented-beak (Section 8.9.2) and buccal-cone conditions are both stylate-haustellate mouthpart classes that lack palpi, the segmented beak condition possesses features not found in the buccal-cone group. These include a prominent bulging clypeal pump, paired mandibular stylets, ocellar presence and other features indicative of a nonparasitic life-habit. Lastly, the haematomyzid proboscis resembles the rhynchophorate rostrum (Section 8.3.10) to the point that in both cases mandibles are located terminally on long proboscides and are rotated 180° for outward "adduction." Although these structures are used to bore or puncture through tough substrates and originated independently, there are other head- and mouthpart-related differences that differentiate haematomyzids and rhynchophorates according to their respective ectoparasitic and free-living life-habits.

Diversity and Natural History. The buccal-cone mouthpart class consists of small, blind, wingles ectoparasites of eutherian mammals that are sanguinivorous and have dorsoventrally flattened bodies. They are highly adapted to the skin and fur environment of their mammalian hosts and parasitize all mammalian groups except monotremes, marsupials, xenarthran sloths, pangolins, whales and sirenians (Kim 1988). Most (67%) are found on rodents and buccal-cones rarely parasitize carnivores. Although cosmopolitan in distribution they are especially abundant in the Ethiopian Region, where they account for more than 35% of all species (Kim 1988). Members of the buccal-cone class include of all anoplurans and the single mallophagan family, Haematomyzidae, consisting of two species, one on African and Indian elephants and the other on wart-hogs. This taxonomic base translates to a diversity of 16 families, 43 genera and 493 species (Appendix D), corresponding to a rank-order of 31 out of 34 mouthpart classes (Table 5, Fig. 131). Kim and Ludwig (1978) estimate that the total number of anoplurans is probably around 1000, once all Recent mammals are inventoried for their parasites. Consequently the buccal-cone class is relatively unimportant as a component of the Recent insect fauna and is one of five stylate-haustellate mouthpart classes that are exclusively or dominately sanguinivorous. Of these, only siphonostylates (Section 8.9.10) have less taxonomic diversity; the buccal-cone class is surpassed by the hexastylate, tristylate and tubulostylate mouthpart classes (Sections 8.9.7 to 8.9.9). Members of the buccal-cone class represent two clade, the Anoplura and the Haematomyzidae-containing Rhynchophthiraptera, that have independently acquired similar mouthpart structures from a common trichodectid, epidermis-chewing mallophagan ancestor probably parasitic on early eutherian mammals (Richards and Davies 1977).

All buccal-cone members are obligate sanguinivores feeding on subcutaneous blood and probably lymph on a wide variety of eutherian hosts (Fig. 101). They apparently are capable of penetrating thick, cornified hides of several ungulate and pinniped groups as well as the thinner integument of smaller terrestrial animals. Very little is known of the feeding of these forms, although the human louse *Pediculus humanus* Linneaus has been studied extensively. *P. humanus* feeds every six hours as a first instar nymph and every three hours as an adult (Hocking 1971). Each male takes from five to 30 minutes for a feeding

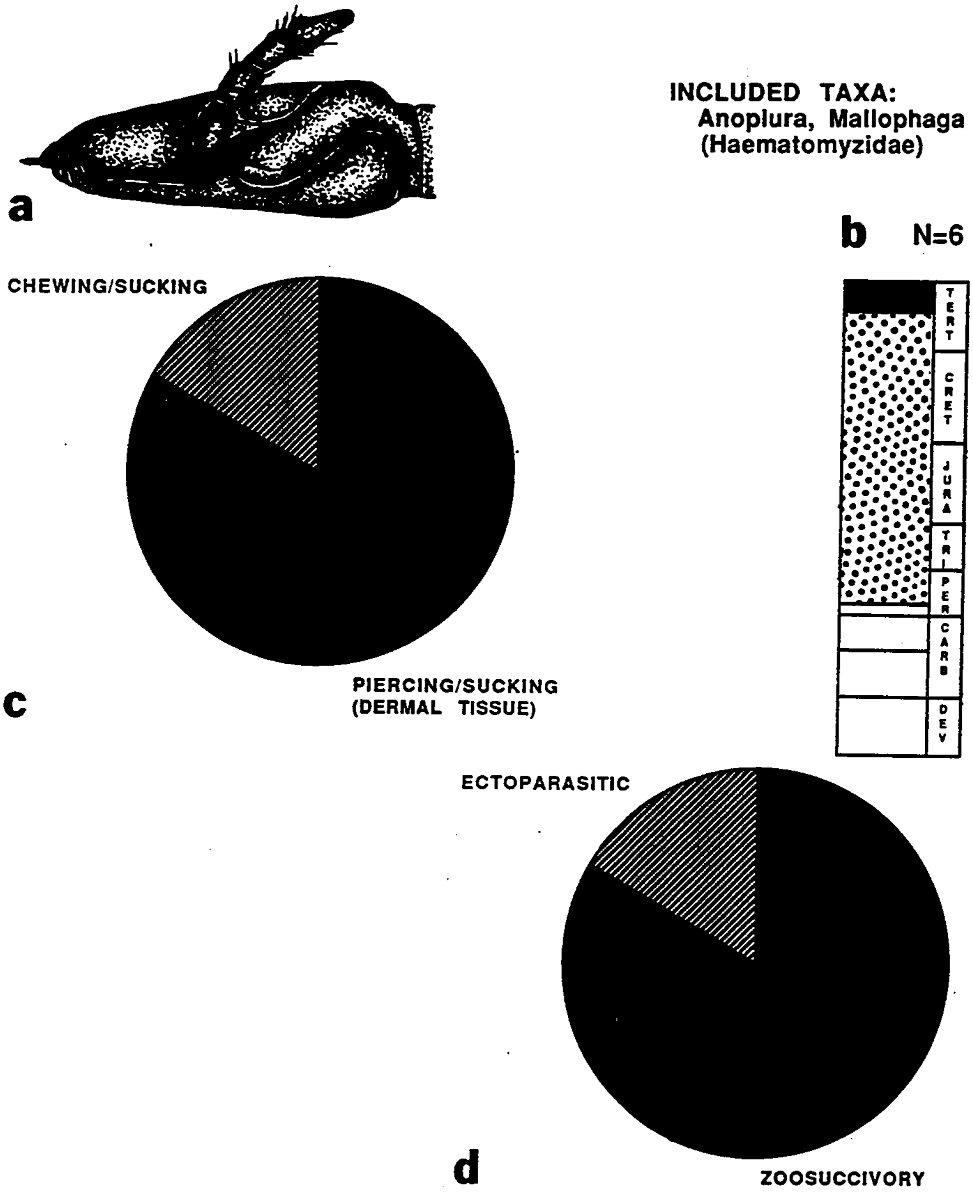


FIGURE 101. Overview of the Buccal Cone Mouthpart Class. a, *Haematopinus suis* (Linneaus) (Anoplura: Haematopinidae, data-set no. 194); b, taxonomic distribution, number of taxa examined and geochronologic history; c, functional-feeding-groups; d, dietary spectrum.

event and the volume ingested may comprise from one-fourth to one-third of the louse's body weight (Murray et al. 1965). The human louse survives less than a day without feeding, although certain seal lice can survive up to several weeks and most other lice can survive a few days without feeding (Marshall 1987). Mammals react to anopluran predation by an increase in skin thickness and a decrease in subcutaneous arteriole density (Nelson et al. 1972).

The Haematomyzidae of the Rhynchophthiraptera is poorly understood when compared to anoplurans, The haematomyzid *Haematomyzus elephantis* Piaget infest integumentary folds in the groin, armpit, ear and root of the tail of the Indian elephant (Murkerji and Sen-Sarma 1955). Farenholz (1936) and Symmons (1952) considered the Rhynchophthiraptera as a suborder of the Anoplura, whereas Mukerji and Sen-Sarma (1955) elevated the taxon to a separate order. Recently the Rhynchophthiraptera has been considered a structurally unique suborder of the Mallophaga (Richards and Davies 1977, Kim and Ludwig 1978, Kim 1980).

Structural Themes. Two basic structural themes exist within the buccal-cone mouthpart class. The first theme comprises all anopluran taxa (Subcluster 1, data-set taxa 194 to 198 in Fig. 102), whereas the second theme consists of the single taxon *Haematomyzus elephantis* Piaget (214). A comparison of these two themes reveals that there are differences in general head and mouthpart characters: for example, the antennae in anoplurans are filiform whereas they are serrate for the haematomyzid and the mouthparts are haustellate and distylate for anoplurans and nonhaustellate and monostylate for haematomyzids.

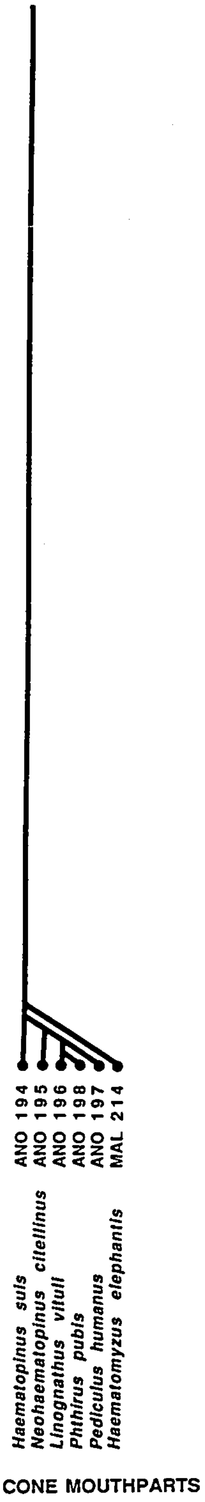


FIGURE 102. Cluster analysis dendrogram of taxa comprising the Buccal Cone Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

Anoplurans possess a quadrate, undivided clypeus whereas haematomyzids bear a small, transversely-elongate clypeus fused to the frons. The mandibles constitute the wall of the oral cone in anoplurans and are functional, trophic structures in haematomyzids; laciniae are absent in anoplurans and present in haematomyzids. Other differences occur. It is likely that these two themes are strongly associated with the structure of the host integument. Rhynchophoran-like rostral elongation (Section 8.3.10) in haematomyzids is a special adaptation for puncturing or possibly boring the hide of pachyderms and contrasts with shorter mouthpart of anoplurans on generally thinner-skinned hosts.

Geochronologic History. The only described fossil of the buccal-cone mouthpart class is the Pleistocene haematopinid *Neohaematopinus relictus* Dubinin from the USSR (Laurentiaux 1953) (Fig. 103). Thus the fossil record is of no assistance in establishing the timing of appearance of major bucal-cone taxa. Kim (1988) in a cladistic analysis of 39 morphological structures supported the conclusion of Kim and Ludwig (1982) that anoplurans may have had an origin as early as the Late Cretaceous. Additionally Kim (1988) concluded that there was minimal concordance between the family-level parasite phylogeny of the Anoplura and the order-level host phylogeny of eutherian mammals, indicating that the original colonization of mammals by anoplurans occurred in a spatiotemporally erratic mode and took place before major cladogenetic events of their hosts. After this initial flurry of host colonization anoplurans apparently coevolved with their host associations. Evidence for this two-phase model is the low level of congruence between

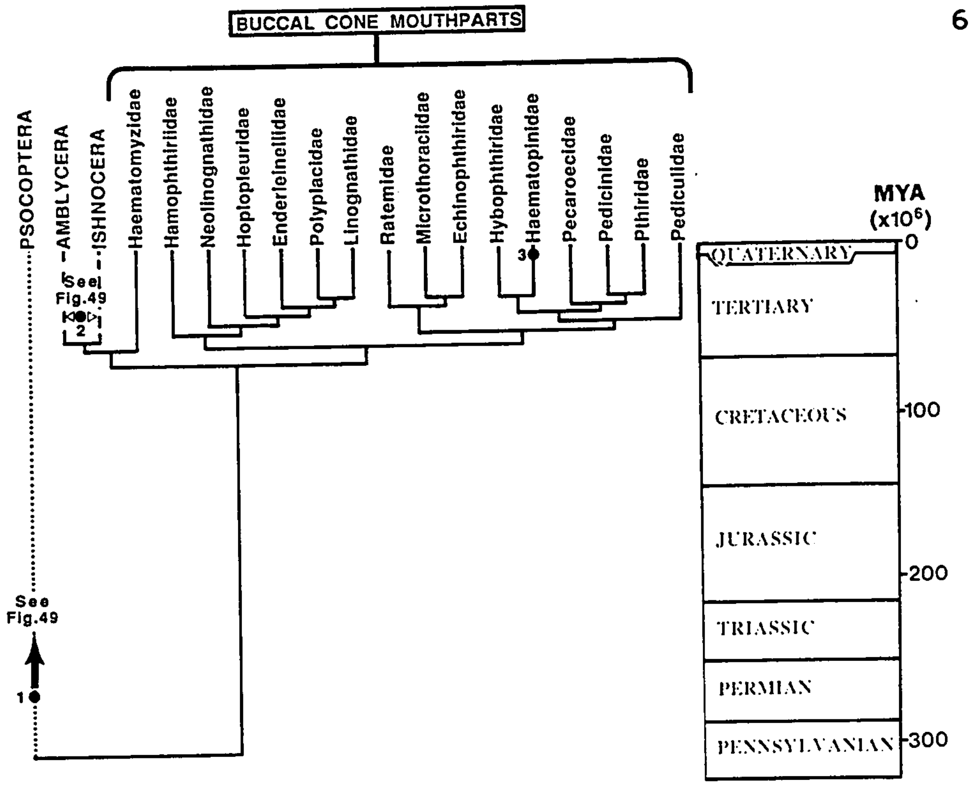


FIGURE 103. Geochronologic history of the Buccal Cone Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Kim (1988) with time value of clades from Kim and Ludwig (1978), based on host phylogeny in the absence of a significant fossil record. The taxonomic level of analysis is the family. The outgroup is Psocoptera.

phylogenies of parasite *families* and host orders, but the high level of congruence between phylogenies of parasite *genera* and host orders (Kim 1988). Approximately 68% of buccal-cone species are confined to a single host; 26% are specific to two or three closely-related host species.

Current ideas for the origin of anoplurans and rhyncho phthirapterans center on a Late Cretaceous (Waage 1979, Kim 1988) or Early Tertiary (Kim and Ludwig 1978, Traub 1980b) origin, the latter contemporaneous with the adpative radiation of Early Tertiary eutherians (Van Valen 1971, Eisenberg 1981). However several synapomorphies unite the Mallophaga and Anoplura (Kristensen 1981) and the closest sister-group of this clade is the Psocoptera, which first appears during the Early Permian (Section 8.3.8). Waage (1979) indicates that the parent mallophagan stock was likely a psocopteran-like nest associate feeding on vertebrate frass (Weber 1939) that subsequently became phoretic on the host and eventually became a facultative consumer of host epidermis. Later, with modification of mandibulate mouthparts into stylate ones, this lineage became an obligate sanguinivore (Waage 1979). In this proposed life-habit transformation series, host/parasite intimacy is maintained continuously and in tandem with gradual selection of more nutritive foodstuffs. This is indicated by a higher rate of egg production in anoplurans than in mallophagans (Murray 1979). Nevertheless the possibility remains that Mallophaga + Anoplura may have cladogenetically separated from the Psocoptera relatively early and during the Early Mesozoic (see Traub 1980b), for which the probable ectothermic and fur-covered therapsids were available as suitable hosts to colonize.

The current absence of members of the buccal-cone class in plesiomorphous mammalian clades, such as monotremes and marsupials, however mitigates against such a hypothesis.

Previous Designations. Because of the small size of anoplurans, their mouthparts were not extensively discussed until the 1800's. Although Hooke (1665) excellently illustrated the structure of an anopluran "snout" in a monograph of microscopic animals, anoplurans did not become widely known until 1826, when Kirby and Spence used the term "Aptera" to refer to a class of insects (including anoplurans) that bore haustellate mouthparts. In 1919 Peacock described the anterior mouthpart region of *Pediculus humanus* Linneaus as a haustellum, although many of the terms used to describe haustellar structures were preceded by the adjective, buccal. Later Fernando (1934) used the same terminology to describe the ontogeny of the same species. Since these initial descriptions of anopluran mouthpart structure there has been no consistent use of a term to describe the anterior, stylet-protecting, conical structure of the anopluran or haematomyzid head. Metcalf (1929) and Matsuda (1965) used the term haustellum, whereas Denis and Bitsch (1973) variously referred to the same structure as a rostrum, haustellum or proboscis (Table 6). Recently, the term proboscis was used by Hirsch (1986) whereas Chaudonneret (1989a) used the term rostrum. Because of the uneveness of terminological application, I am applying the term **buccal-cone** to refer to the anterior projection of anopluran and haematomyzid heads and as a name for their encompassing mouthpart class. Other terms, such as haustellum, rostrum, or proboscis either have utility as broader-scale descriptors of mouthpart structures, or they are preoccupied as names of other mouthpart classes (see Section 8.3.9 for rostrate).

Review of Literature. Data for description of buccal-cone mouthparts is limited. However several major treatments of mouthpart structure of selected species include Peacock (1919) for the pediculid *Pediculus humanus* Linneaus; Stojanovich (1945) for the haematopinid *Haematopinus suis* (Linneaus), the hoplopleurid *Neohaematopinus citellinus* Ferris, the linognathid *Linognathus vituli* (Linneaus) and *P. humanus*; Mukerji and Sen-Sarma (1955) for the haematomyzid *Haematomyzus elephantis* Piaget; Ramcke (1965) for *P. humanus*; and Hirsch (1986) for the phthirid *Phthirus pubis* Linneaus, known as the crab louse or cootie. Young (1953) surveyed the embryology of representative anopluran species. Shorter descriptions are Fernando's (1934) account of development of mouthpart homologies, Weber's (1938) study of the mouthpart structure of *H. elephantis* and Lavoipierre's interesting account of the feeding mechanism of *H. suis* on arterioles and capillaries of trans-illuminated mouse ear. General reviews of buccal-cone mouthpart structure can be found in Matsuda (1965), Denis and Bitsch (1973), Smith (1985) and Chaudonneret (1989a).

8.9.4. Mouthcone Class
(Class 26)

Description. Head quadrate-spheroidal, asymmetrical; proboscis short, nonretractile. Genae well- to minimally-developed; gula and lora absent. Antennae moniliform; ocelli 3, rarely absent; compound eyes expansive, rarely absent. Mouthparts opisthognathous, housed in a mouthcone, stylate-haustellate with 3 stylets. Food pump clypeal and cibarial.

Clypeus quadrate, infrequently otherwise, subdivided into 2 sclerites. Labrum quadrate or transversely-elongate, undivided, with aperturate margin. Hypopharynx with superlingulae, two ovoidal sclerites and a median, basal sitophore; epipharynx membranous or forming the ventral part of a food pump. Left mandible stylate, edentate, protractile, characterized by modified protraction/retraction; right mandible absent. Maxilla with basal undifferentiated sclerites, bearing a mouthcone wall element, palp and lacinial stylet. Maxillary palp 2- or 3-segmented; filiform, rarely pectinate; intermediate in length. Galea part of mouthcone wall; lacinia grooved, stylate and acuminate. Labium with two elongated basal segments, mouthcone wall elements and palps. Labial palps 1-segmented, rarely otherwise; filiform, rarely stubby; short to intermediate in length. Glossae and paraglossae part of mouthcone wall. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. The Mouthcone Mouthpart Class is distinctive and bears several major features that are unique to the class. The most important feature is the pronounced asymmetry of the head capsule and mouthpart elements. This major asymmetry is expressed by the accomodating, trapezoidal shape of the clypeal and labral sclerites, absence of the right mandible and enlargement of the wall-forming mouthcone sclerites of the left maxilla at the expense of the right maxilla. Mouthcones are the only mouthpart type that bear a single mandible.

Additionally this class uniquely has structures that are found in both typical mandibulate groups and in derived stylate-haustellate groups. Particularly notable is the singular combination of stylate mouthpart elements (mandible, laciniae) and *two* pairs of well-formed maxillary and labial palps. Also the unique structure of the mouthcone is derived from evident clypeal, labral, labial and basal mandibular and maxillary sclerites that fuse to form the lateral walls of the funnel-shaped mouthcone. The mandibular stylet is not protracted by a lever-based system as in segmented-beaks (Section 8.9.2), but is literally pulled down for retraction by a muscle attached to a mandibular guide from the anterior clypeus. The antennae are characteristically moniliform.

Comparisons of the Mouthcone Mouthpart Class can be made to the Buccal-Cone Mouthpart Class (Section 8.9.3) and certain members of the Entognathate Mouthpart Class (Section 8.3.2). Both buccal-cones and entognathates have symmetrical cephalic capsules, a pair of nonstylate mandibles and a well-developed gular region. Other stylate-haustellate mouthparts (Section 8.9) lack well-formed maxillary palps and substitute either a stylet-enclosing labial sheath (modified palpi) or a galeal siphon as the structures involved in piercing, instead of a mouthcone whose sidewalls are composed of sclerites from major mouthpart regions.

Diversity and Natural History. The Mouthcone Mouthpart Class consists of small (generally 0.5 to 8mm long), slender-bodied insects that are not prone to flight, and occur on vegetation and fungi, in rotting wood, in leaf litter and under bark. They are an old group, originating during the Late Paleozoic and apparently evolved a form of holometaboly, replete with a pupal stage, independent of the Oligoneoptera (Richards and Davies 1977). The mouthcone class is coextensive with the order Thysanoptera and undoubtedly represents a monophyletic group. Although the mouthcone is an unique mouthpart-housing structure, some entognathate collembolans (Adams and Salmon 1972; Section 8.3.2) and buccal-cone anoplurans (Hirsch 1986; Section 8.9.3) have analogous structures that are reminiscent of mouthcones. Mouthcones comprise five families, 550 genera and 8800 species (Appendix D) and has a rank-order of 16 out of 34 mouthpart classes (Table 5, Fig. 131). Their role in the modern insect fauna is relatively minor although locally they are important pollinators and fluid-feeders of plant tissues. Their principle ecological competitors are those members of the Segmented-Beak Mouthpart Class (Section 8.8.2) that possess short beaks and stylets and are able to feed on shallow, nonvascular plant tissue. Both mouthpart groups and a few other components from other stylate-haustellate mouthpart classes, are frequently combined into the ecologically important sap-sucking guild (Moran and Southwood 1982, Stork 1987).

All members of the mouthcone class can be placed into the following dietary categories, in decreasing order of frequency: live plant tissue (herbivory), pollinivory, fungivory, carnivory and nectarivory (Fig. 104). (For accounts of the feeding mechanism and behavior of members of the mouthcone class, see Grinfel'd [1959], Heming [1978] and Smith [1985].) Most mouthcone members imbibe fluid cellular contents by puncturing the outer integument of plant tissue by inserting a single mandibular stylet and then appressing paired, grooved lacinial stylets into a tubular hole that is used for sucking up intercellular or

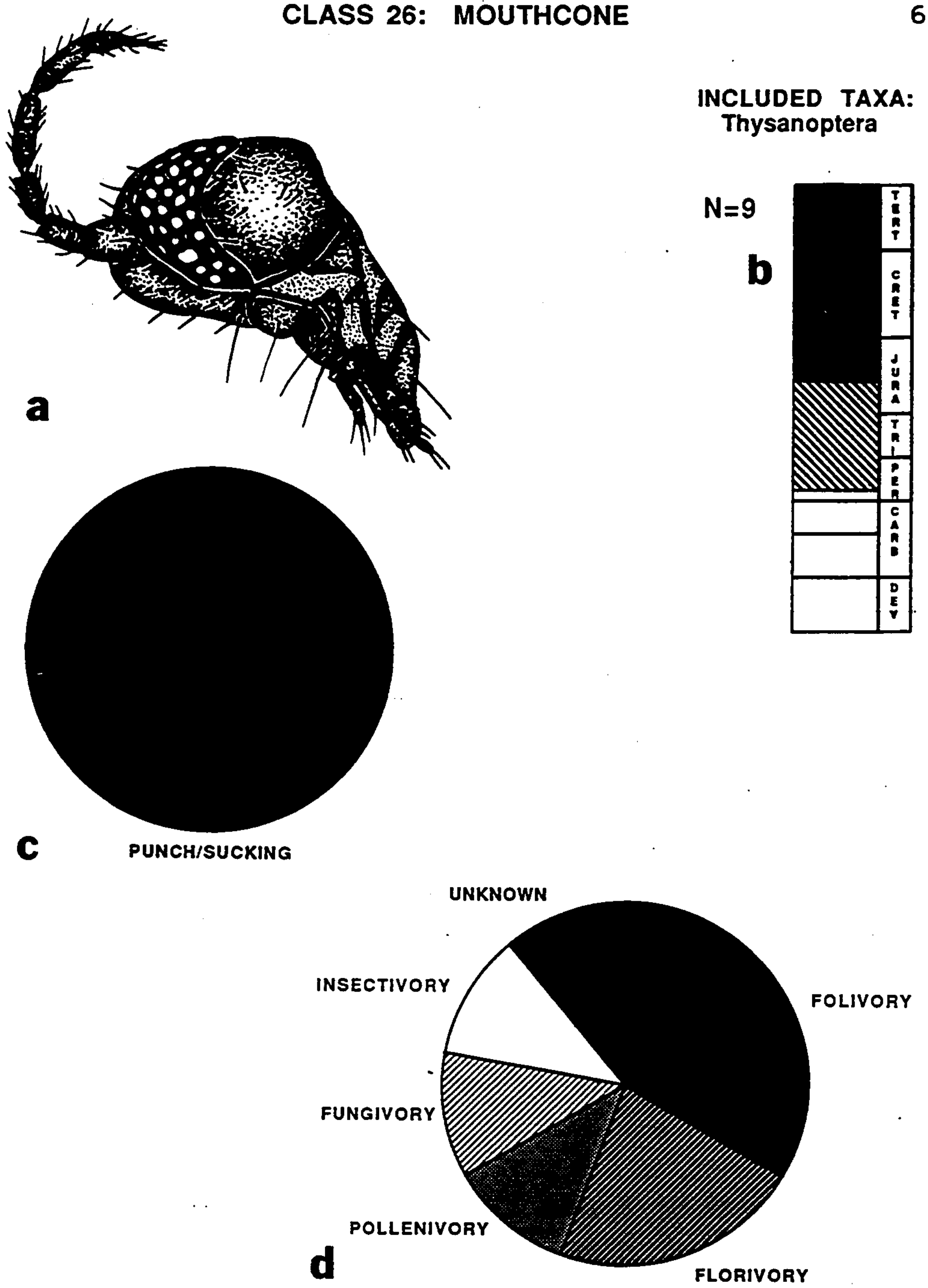


FIGURE 104. Overview of the Mouthcone Mouthpart Class. a, *Aeolothrips fasciatus* Linneaus (Thysanoptera: Aeolothripidae, data-set no. 215); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-group; d, dietary spectrum.

intracellular fluid (Heming 1978). Although the food tube of the conjoined lacinial stylets is about lum in diameter, chloroplasts as large as six um in diameter can be imbibed without rupture; in fact, the protoplasts of many mesophyll and epidermal cells are consumed with a minimum of seepage after stylet withdrawal (Chisholm and Lewis 1984). Some large species can consume particulate matter such as algal cells or spores from 10 to 30um in diameter (Grinfel'd 1959). Most herbivorous mouthcone class members consume buds, flowers and catkins (Barbosa and Wagner 1989) and, unlike the homopteran members of the segmented-beak class, mouthcone members primarily feed on regions of the plant that are rich in proteins and sterols such as meristematic tissue and reproductive organs (Southwood 1973). Many mouthcone members induce galls on these plant regions (Frost 1959) and gall plants such as *Acacia* (Fabaceae). Genera such as *Kladothrips* are known to be widespread gall-formers (Mound 1971). In addition to inducing galls several mouthcone species transmit viruses that frequently have major negative effects on plant health (Barbosa and Wagner 1989).

Although it was once believed that members of the mouthcone class were overwhelmingly or exclusively feeders on live or dead vegetation, relatively recent research has demonstrated that pollinivory is at least the second most common nutritional source. The first extensive description of this phenomenon was by Grinfel'd (1959) who described the stereotyped punch-and-suck feeding technique of thysanopterans. According to Grinfel'd (1959), and later corroborated by other researchers (Lewis 1973, Heming 1978, Chisholm and Lewis 1984), thysanopterans initially secure a pollen grain with their labial and maxillary palps and then thrust a single mandibular stylet onto its surface as the grain is pressed against the oral cone. This is followed by deployment of the lacinial stylet tube which is used for suction of the internal protoplast. Kirk (1984) has determined that the feeding time per grain is positively associated with grain volume and very large grains and grain tetrads are frequently abandoned before completion of feeding. Kirk also found that large amounts of pollen can be consumed by a single individual, up to 100 pollen grains per 15 minutes. He later (1985) ascertained that some floricolous thysanopterans were capable of feeding on a wide variety of pollen sizes and ornamentations; other species were host-specific and, unlike the generalists, were able to detect their hosts without tactile probing. Although pollen consumption renders a positive effect on thysanopterans by the production of greater egg number (Kirk 1985), the plant receives benefit by being pollinated.

Members of the mouthcone class consume the pollen of gymnosperms (Lewis 1973, Anathakrishnan 1979), primitive magnoliid dicots (Thien 1980, Bernhardt and Thien 1987) and various derived nonmagnoliid dicots (Proctor and Yeo 1973, Faegri and van der Pijl 1980). The occurrence of mouthcones as pollinators of such plesiomorphic angiosperms as the magnoliid families Winteraceae (Thien 1980), Myristaceae (Bernhardt and Thien 1987) and Monimaceae (Gottsberger 1977) suggests that the mouthcone class was an important pollinator group in primitive angiosperms along with co-occurring coleopterans and dipterans (Thien 1980, Kevan and Baker 1984). Also, the presence of members of this mouthpart class as dominant or subdominant pollinators on several apomorphic, nonmagnoliid families such as the Dipterocarpaceae (*Shorea*: Ashton 1977, Appanah and Chan 1981), Chenopodaceae (*Beta*: Proctor and Yeo 1973), Polemoniaceae (*Phlox*: Faegri and van der Pijl 1980), Solanaceae (*Solanum*: Velayudhan and Annadurai 1986), Fabaceae (*Medicago*: Faegri and van der Pijl 1980), Ranunculaceae (*Anemone*: Proctor and Yeo 1973) and Ericaceae (*Erica*, *Calluna*: Hasterud 1974) implies that thysanopterans (i.e. mouthcones) are probably the most important pollinators group after the "big four" of Coleoptera, Diptera, Lepidoptera and Hymenoptera (see also Porsch 1958). Members of the mouthcone class should be suspected as pollinators of small, perfect flowers with anthers located above the stigmatic surface.

Fungivorous mouthcone members are found in a diversity of environments, principally cryptic habitats among microscopic fungi associated with rotting wood and herbivore dung. They also occur in exposed areas that harbor macroscopic fungi such as the sporocarps of polypores and mushrooms (Hamilton 1978, Kukor and Martin 1987). Anathakrishnan and Suresh (1983) described Indian species that exhibit diverse feeding specializations on fungal food; species such as *Tiarothrips subramanii* (Ramakrishna) for example prefer ascomycetan spores (Anathakrishnan and James 1983). Some fungivorous members may be obligate mycetibionts in large sporocarps.

The last two dietary categories, insectivory and nectarivory, are less well known. Frost (1959) and Richards and Davies (1977) indicate that phlaeothripids consume aphids, mites and insect eggs. The imbibation of nectar and exuding plant sap was mentioned by Grinfel'd (1959) and Brues (1972).

The mouthcone class is a minor component of the sap-sucking feeding guild in modern ecosystems. As a percentage biomass contribution to all herbivores consuming particular plants, members of the mouthcone class range from one percent in the case of *Ceanothus velutinus* (Rhamnaceae) in western Oregon (Schowalter et al. 1988), to four percent in the case of *Cirsium* thistles (Asteraceae) in southern California (Goeden and Ricker 1987b). Mouthcone class components of sap-sucking guilds also occur in cool-temperate mesic forest (Moran and Southwood 1982) and tropical rainforest (Stork 1987), although their proportional representation was not recorded.

Structural Themes. Two demonstrable, structurally interpretable subclusters are evident in Fig. 105. The first subcluster, comprising one aeolothripid and four thripid taxa (data-set taxa 215 to 218 in Fig. 105) consists of herbivorous forms that feature prominent, well-developed genae, a membranous epipharynx, maxillary palps that are usually three-segmented and a tendency toward intermediate-length labial palps. By contrast the second subcluster consists of one aeolothripid and three phlaeothripid taxa (221 to 216) that are insectivorous forms. This subcluster comprises taxa that are typified by genae that represent an expansive separation of the eyes from the mouthparts, an epipharynx contributing to formation of the ventral region of the food pump, two-segmented maxillary palps and a tendency toward short labial palps. The structural differences between these two themes are not pronounced, involving only several characters, and is probably associated with the two major modes of feeding: herbivory *sensu lato* and insect predation.

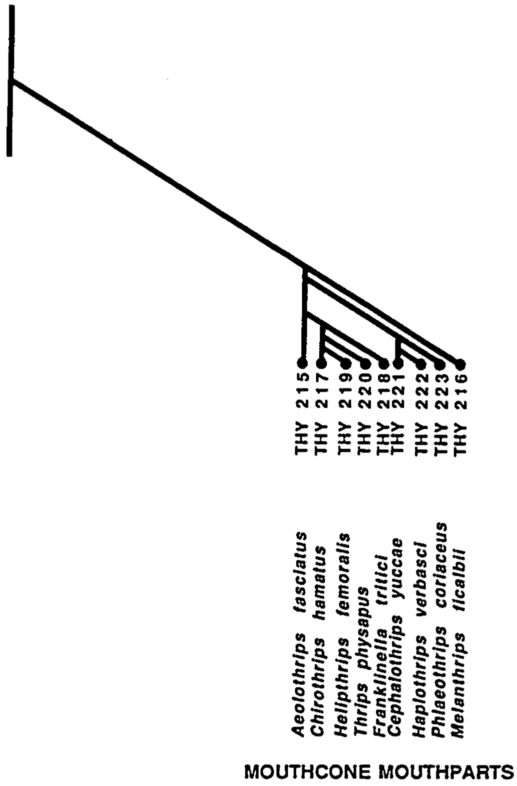

THY 215 Aeolothrips fasciatus
THY 217 Chirothrips hamatus
THY 219 Helipthrips femoralis
THY 220 Thrips physapus
THY 218 Frankliniella tritici
THY 221 Cephalothrips yuccae
THY 222 Haplothrips verbasci
THY 223 Phlaeothrips coriaceus
THY 216 Melanthrips ficalbii
MOUTHCONE MOUTHPARTS

FIGURE 105. Cluster analysis dendrogram of taxa comprising the Mouthcone Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

Geochronologic History. I will approach the geochronological history of the Mouthcone Mouthpart Class in two ways. First, the empirical fossil record will be examined; and second, synecological, phylogenetic and structural data will be used to (i) ascertain the life-habits of the ancestral Late Paleozoic mouthcone class progenitor and (ii) establish the role that the mouthcone class probably played in the early evolution of angiosperms. It is hoped that both approaches can be collectively used for establishing the major features of the history of the group.

Although thysanopterans are inferred to have diverged during the Carboniferous from a hemipteran (Homoptera + Heteroptera) sister-group (Fig. 106), the earliest accepted thysanopteran is *Permothrips* Martynov 1938 from the Cherkarda deposits of the USSR [89] (Hennig 1981, but see Strong et al. 1984). This species and other related taxa that span a duration into Late Cretaceous times comprise the family Lophioneuridae. The thysanopteran affinities of the Lophioneuridae have only recently been established by Vishniakova (1981). While lophioneurids lacked the strap-shaped wings fringed by long setae of modern forms and exhibited a somatically robust, psocid facies, Vishniakova (1981) demonstrated (i) the presence of a hypognathous, funnelform (though apparently symmetrical) mouthcone with stylate mouthparts, (ii) compound eyes with individually-facetted, bulbous ommatidia and (iii) incipient development of marginal alar setae, which indicate the thysanopteran affinities of this clade. Lophioneurids are represented by *Zoropsocus tomiensis* Bekker-Migdisova 1961 from the Upper Permian deposits of the Kusnetsk

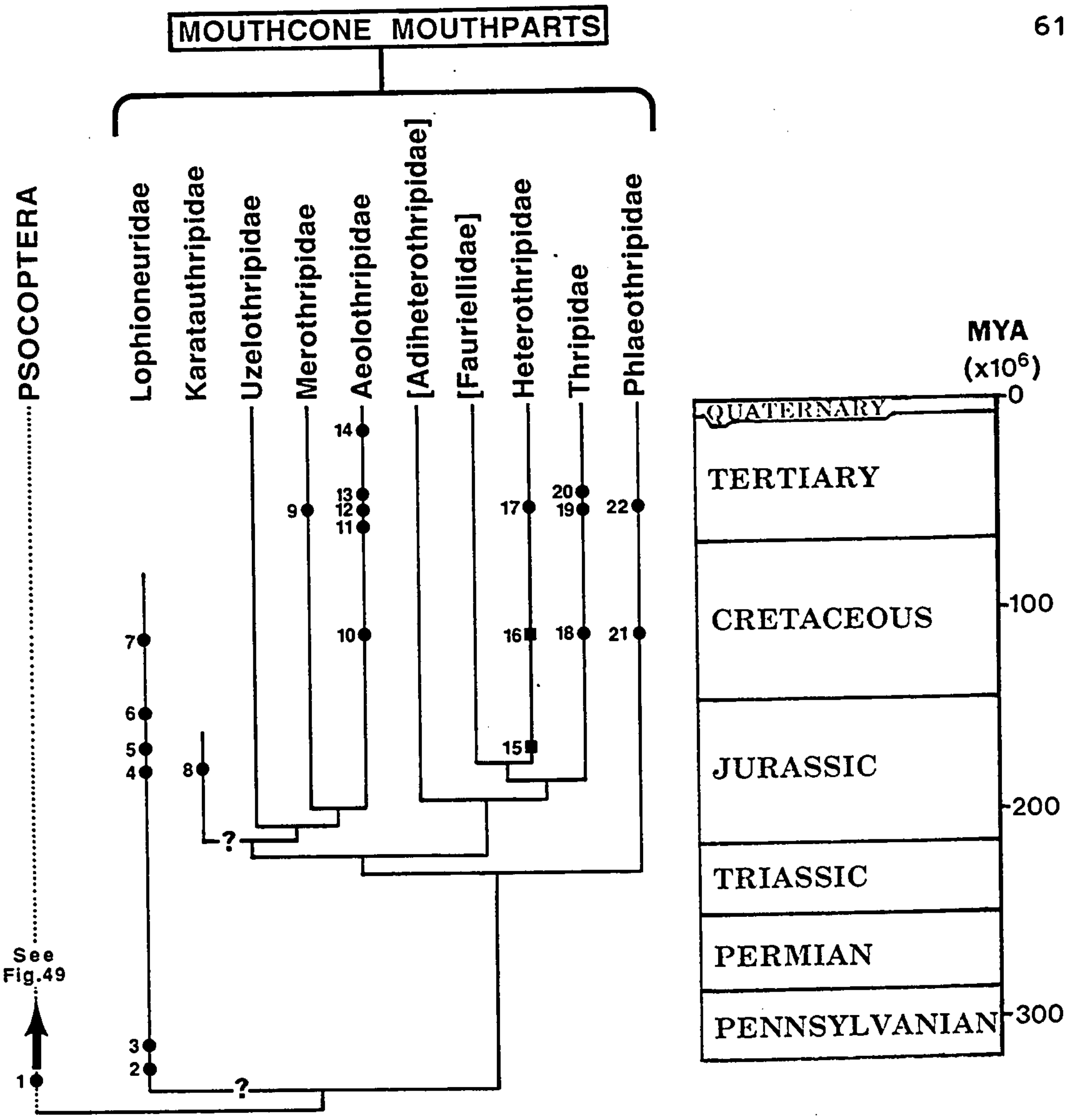


FIGURE 106. Geochronologic history of the Mouthcone Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Mound et al. (1980), Hennig (1981) and some aspects of timing after Sharov (1973) and Seeger (in Hennig, 1981). The taxonomic level of analysis is the family. The outgroup is Psocoptera. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

Basin, USSR [97] and reappear in Upper Jurassic deposits of the USSR [60] (Vishniakova 1981). After a several post-Jurassic occurrences, they are last found in Late Cretaceous Siberian amber [37] (Zherikin and Sukacheva 1973). This group was considered as possibly pollinivorous by Strong et al. (1984).

During the Jurassic a diversification of the presumed sister-group of the Lophioneuridae occurred, resulting in the appearance of at least three modern-aspect families by Late Cretaceous times. These are the Aeolothripidae, Thripidae, Phlaeothripidae and possibly the Heterothripidae, recorded from Late Cretaceous Siberian ambaer [37] (Zherikin and Sukacheva 1973, Rasnitsyn 1988). However, the description of five extinct families in earlier Lower Cretaceous Lebanese amber [55] by Zur Strassen (1973) has been reinterpreted by Seeger (in Hennig 1981) as unwarranted because of the lace of demonstrable apomorphies for credible diagnoses. These forms are probably heterothripids or members of the sister-group to the Heterothripidae + Fauriellidae. Subsequent mouthcone class members have been abundantly documented from Early Tertiary Baltic amber [19] (Priesner 1924, Larsson 1979) when merothripids and demonstrable heterothripids enter the record.

Several models exist for the feeding-and life-habits of the ancestral thysanopteran or mouthcone class member. Grinfel'd (1959) maintained that predatory feeding is primitive and modern thysanopteran groups switched protein food sources from insects to pollen. Stannard (1968) and Anathakrishnan (1979) held that thysanopterans are most parsimonously treated as primitively herbivorous, with fungivory subsequently derived several times. Mound and O'Neill (1974) and Mound et al. (1980) maintained that fungivory in litter is plesiomorphous and that herbivory, predation and fungivory under bark are all apomorphic life-habits. Confirmation of these hypotheses can be assisted by ascertaining the life-habits of the ancestral hemipteran, which itself is a debated issue (Mitter et al. 1988; Section 8.9.2).

Members of the mouthcone mouthpart class were available during the Early Cretaceous for pollination of some of the earliest known angiosperm clades (Gottsberger 1988), notably the Chloranthaceae whose record commences during the Barremian (Walker and Walker 1984), the Winteraceae commencing during the Albian/Aptian (Crepet and Friis 1987) and the Monimaceae during the Turonian (Friis 1989). All of these clades have extant representatives that are pollinated by thysanopterans (Gottsberger 1977, Thien 1980, Pellmyr and Thien 1986). This pattern implies that early angiosperm flowers were probably small and inconspicuous, and pollinated by unspecialized opportunists such as thysanopterans, beetles and some generalized dipterans (Bernhardt and Thien 1987) and not faithful pollinators such as members of the siphonate and glossate mouthpart classes.

Previous Designations. Although mouthcone mouthparts are structurally distinctive, there was no mention of them in the literature until the late 1800's. Early entomologists such as Fabricius, MacLeay, Kirby and Spence, and Latreille failed to include thysanopteran mouthpart structures in any of their keys of the Insecta--an oversight that is probably attributable to thysanopteran small size. Although Jordan

(1888) monographed the Thysanoptera (his Physopoda) and illustrated all the essential features of the mouthcone, he only hinted at the possibility of cephalic and mouthpart asymmetry. It was not until 1896 that Garman explicitly mentioned the occurrence of asymmetry in thysanopteran mouthparts. This point was re-emphasized by Borden in 1915.

The earliest documented use of the term mouthcone was by Peterson (1915) although it may have had a previous informal history. In Metcalf's classification of hexapod mouthparts (1929), the thysanopteran condition was termed the "rasping-sucking type" of his Haustellate Series. This designation was retained in Metcalf et al. (1962), although James and Harwood (1969) used "thysanopteran type" to refer to the same mouthpart type. Recently, Borror et al. (1976) referred to thysanopteran mouthparts as "haustellate type: mouthparts of thrips." In a recent series of articles treating mouthpart types in hexapods, Chaudonneret (1989a) considered the mouthparts of thysanopterans (*l'appareil piqueur des Thysanoptères*) as a unique type of piercing mouthpart apparatus and used *Aeolothrips* and *Haplothrips* as exemplars. All of these characterizations use functionally- or taxonomically-related terminology to name what I consider a structural feature. For this reason I am using the struc tural term **mouthcone** as a name for the mouthpart class described herein.

Review of Literature. Sources of data on mouthcone mouthparts are principally treatments focusing on the mouthpart structure of one or a few taxa, review articles of the mouthpart structure for the Thysanoptera as a whole, shorter works detailing the function and structure of particular head or mouthpart elements and various taxonomic monographs that discuss mouthpart structure of selected taxa in passing. Treatments focusing on the mouthpart structure of one or a few taxa include Borden (1915) for the thripid *Frinklinella tritici* (Fitch), Peterson (1915) for the thripids *Heliothrips femoralis* (Reuter) and *Thrips physapus* Linneaus and the phlaeothripid *Cephalothrips yuccae* Hinds, Reyne (1927) for the thripids *Dinothrips sumatrensis* Bagnoll, *Heliothrips haemorrhoidalis* Bouchè and *Selenothrips rubrocincta* Giard, Jones (1954) for the thripid *Chirothrips hamatus* (Trybom), Risler (1957) for the *T. physapus*, Mickoleit (1963) for the aeolothripid *Aeolothrips fasciatus* Linneaus and the phlaeothripid *Phlaeothrips coriaceus* (Haliday), Heming (1978) for the nymph of the phlaeothripid *Haplothrips verbasci* (Osborn) and Moritz (1989) for the thripid *Hercinothrips femoralis* (Reuter). These studies, many of them classic, focused on only three thysanopteran families and several of the genera were examined intensively more than once by different authors. Members of poorly-known families, such as Heterothripidae and Merothripidae are desperately in need of study. Shorter studies include Garman (1896) who noted the asymmetry of thysanopteran mouthparts, Davies (1958) who made general observations on the head and mouthparts of *Limothrips cerealium* Haliday and Mound (1971) who compared the feeding apparati and stylet structure of several thysanopteran groups. General reviews of mouthcone mouthparts can be found in Matsuda (1965), Denis and Bitsch (1973) and Smith (1985).

Monographic-size taxonomic works in which mouthpart structure of selected taxa are mentioned in passing include Jordan (1888) and Doeksen

(1941) who provided general overviews of the structure and anatomy of several selected thysanopteran taxa and Mound (1971) who reorganized phlaeothripid systematics and emphasized stylet structure. Studies with scanning electron micrographs of head and stylet struc ture are Heming (1978) for *Haplothrips verbasci* (Osborn), Weisenborn and Morse (1988) for *Scirtothrips citri* (Moulton), and Moritz (1989) for *Hercinothrips femoralis* (Reuter).

8.9.5. Monostylate/Distylate Class (Class 27)

Description. Head quadrate or vertically prolonged; proboscis long to very long. Genae and gula prominent and well- to minimally-developed; raptorial prothoracic legs often present. Antennae mostly stylate, uncommonly filiform; ocelli 3; compound eyes expansive and large. Mouthparts prognathous, stylate-haustellate, monostylate or distylate, nonretractile. Food pump clypeal and pharyngeal.

Clypeus quadrate, rarely transversely elongate; fused to frons. Labrum vertically very elongate, less commonly transversely-elongate; undivided; margin mucronate to uncommonly triangular-acute; part of labellum. Hypopharynx long and stylate, rarely otherwise; epipharynx membranous. Mandibles absent. Maxilla with basal sclerite elongated; bearing a lacinia and palpus only. Maxillary palpus 1- or 2- segmented; brushlike, rarely filiform or stubby; mostly intermediate to long. Lacinia elongate and fleshy or an acuminate stylet; galea absent. Labium with main-body of two sclerites, shape variable; glossae and labial palps present. Labial palps 2-segmented, an appressed palpal structure, rarely aciculate; of intermediate length. Glossae papillate to rarely generalized or absent; paraglossae absent. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. Monostylate/Distylates are the only mouthpart class with the combination of (i) an elongate dipteran haustellum of appressed palps without a distal fleshy expansion and (ii) presence of either one or two haustellar stylets. These are the only discrete characters that consistently define the monostylate/distylates.

Monostylate/distylates have a basic dipteran head and mouthpart facies that is distinguished from other similarly appearing dipteran mouthpart classes, namely distylate/tetrastylates, hexastylates and labellates. The monostylate/distylate class bears a nonretractile, elongate, prognathous haustellum whereas the distylate/tetrastylate class has a retractile, stouter, hypognathous labellum typical of astylate labellates (see Sections 8.5.3 and 8.9.6). The epipharynges of monostylate/distylates is membranous whereas those of distylate/tetrastylates are stylate. Hexastylates have proboscides similar to monostylate/distylates, except that they bear six instead of one or two stylets. Labellates, tubulostylates and siphonates lack lacinial or hypopharyngeal stylets.

Diversity and Natural History. The monostylate/distylate mouthpart class consists of medium-sized adult brachycerans that are strong fliers and diurnally active. They occur in well-lighted terrestrial habitats such as grassland, woodland and water edges but not in dark, canopied forest. As a class they are bimodal in food habits, feeding on insect prey or imbibing nectar and occasionally pollen (Fig. 107). Monostylate/distylates are moderately diverse taxonomically, comprising four families and approximately 745 genera and 12,350 species (Appendix D) and rank 15 out of 34 mouthpart classes (Table 5, Fig. 131). Apparently the mouthpart class is multiply convergent; each monostylate/distylate family originated from more structurally generalized brachycerans that bore mouthparts with a greater number of stylets, or possibly from labellate forms. Stylet reduction and modification of the labium into a prolonged, frequently tubular proboscis (often for anthophily) was a feature of early brachyceran evolution. Monostylate/distylates became a significant predator group (particularly asilids) and an important pollinator assemblage (particularly bombyliids) during the later Mesozoic (after Rohdendorf 1974). Monostylate/distylate pollinators probably antedate the appearance of labellates, siphonates and glossates of more recent Mesozoic history.

Asilids and most empidids comprise the predaceous component of monostylate/distylate taxa. Asilids (robber flies) are predaceous on other insects, rapaceously pursuing they prey in the air and on the ground. They are active during the warmest part of the day, peferring temperatures above 20 degrees C. and occurring on various taxa-specific types of perches, including rock ledges and sandy substrates. Upon capture of prey that may be up to 2.5 times their own size, they use their hypopharyngeal dagger to inject an anaesthetic and proteolytic saliva that digests the contents of their prey from within. This is followed by sucking out the prey contents as it is held securely by raptorial legs. Frequently species of asilids only pursue prey that are

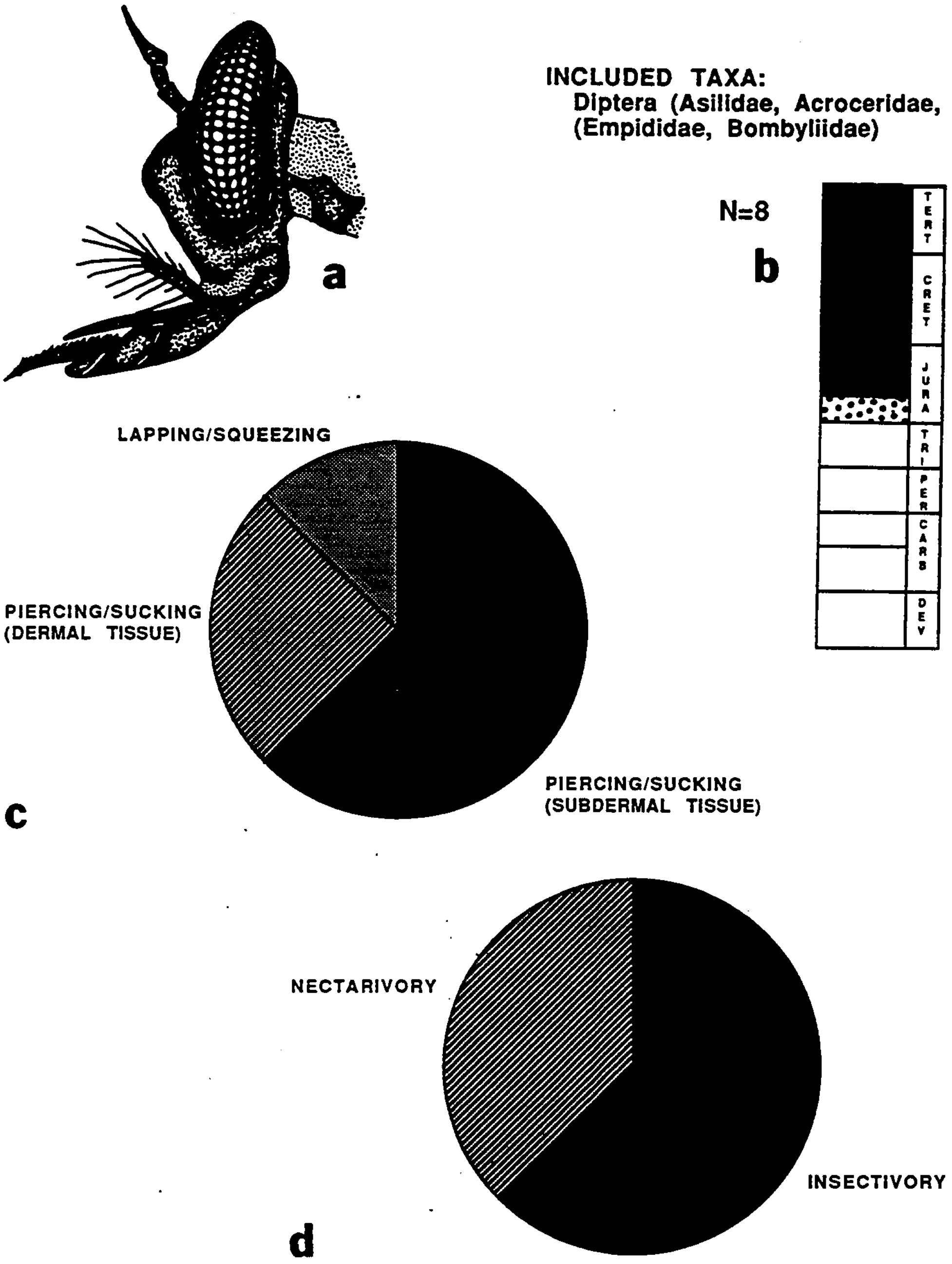


FIGURE 107. Overview of the Monostylate/Distylate Mouthpart Class. a, *Proctacanthus* sp. (Diptera: Asilidae, data-set no. 901), after Snodgrass (1943); b, taxonomic distribution, numbers of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

members of certain orders and of a particular size range (Wood 1981c). Although both sexes of empidids (dance flies) are similarly predatory and insectivorous, they are less agressive in their pursuit and capture behavior and concentrate principally on dipteran larvae and adult nematocerans as prey (Downes and Smith 1969). A few empidids subsist on dead insects such as those found on spider webs. Like asilids, they occur at distinct feeding stations and frequent swarms of nematocerans along river banks or hunt from particular plant surfaces (Steyskal and Knutson 1981). Empidids, unlike asilids, have an unique behavior in which males present dead insect prey to females as a courtship ritual.

Nectarivory and occasionally pollinivory occurs among monostylate/ distylates especially among bombyliids and acrocerids and subordinately in empidids. Bombyliids and some empidids have proboscides up to 1.2cm long and imbibe deeply hidden nectar from small, or long and deep, tubular flowers (Proctor and Yeo 1973, Faegri and van der Pijl 1980) and are important pollinators of these flower types (Grinfel'd 1959, Proctor and Yeo 1973). Bombyliids in particular are among the most highly specialized feeders on floral nectar and possess a forwardly-directed, tubular proboscis that is deployed while hovering above or alighting on flowers (Barth 1985, Willemstein 1987). In some ways bombyliids are convergent upon and compete with diurnal glossates and siphonates (Armstrong 1979). Their common name, bee flies, not only originates from a similar physical appearance to some bees, but also their beelike pollinator behavior. Although bombyliids have been considered flower inconstant as pollinators, even though they perceive color (Faegri and van der Pijl 1980), recent research indicates that they are flower-specific, faithful pollinators (Grimaldi 1988). Some empidids such as *Anthalia* and possibly *Euthyneura*, and several bombyliids are pollinivores (Armstrong 1979, Steyskal and Knutson 1981) and presumably consume the grain intactly. A few empidids have been observed to pierce plant tissues and suck out plant juices (Proctor and Yeo 1973). Acrocerids probe for flower nectar with long proboscides (Rohdendorf 1974, Willemstein 1987) and are probably obligate nectarivores and significant pollinators for some plant species (Schlinger 1981). A few bombyliids (not analyzed in this study) possess abbreviated, distally flaring proboscides (Richards and Davies 1977) and are probably members of the labellate mouthpart class (Section 8.5.3).

Structural Themes. Two principal structural themes characterize the monostylate/distylate class. The first theme consists of an acrocerid, two bombyliids and an empidid (Subcluster 1, bracketed by data-set taxa 896 to 912 in Fig. 108). This theme possesses vertically prolonged heads with long proboscides that bear two stylets only, cursorial prothoracic legs, a vertically very elongate labrum, a maxillary palp that is shorter or longer than intermediate-length and acuminate-stylate laciniae. The second theme comprises only asilids (Subcluster 2, taxa 898 to 902). This theme features a quadrate head capsule, raptorial prothoracic legs, a long proboscis with a single hypopharyngeal stylet, a transversely-elongate labrum, a maxillary palpus of intermediate-length, and elongate but fleshy laciniae. These two structural themes closely correspond to feeding habits. The first theme consists of taxa that are predominately nectarivorous, although

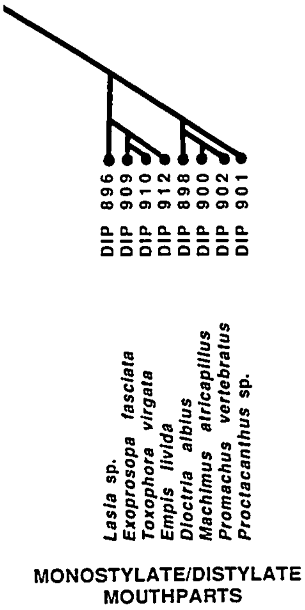

DIP 896 Lasia sp.
DIP 909 Exoprosopa fasciata
DIP 910 Toxophora virgata
DIP 912 Empis livida
DIP 898 Dioctria albius
DIP 900 Machimus atricapillus
DIP 902 Promachus vertebratus
DIP 901 Proctacanthus sp.
MONOSTYLATE/DISTYLATE
MOUTHPARTS

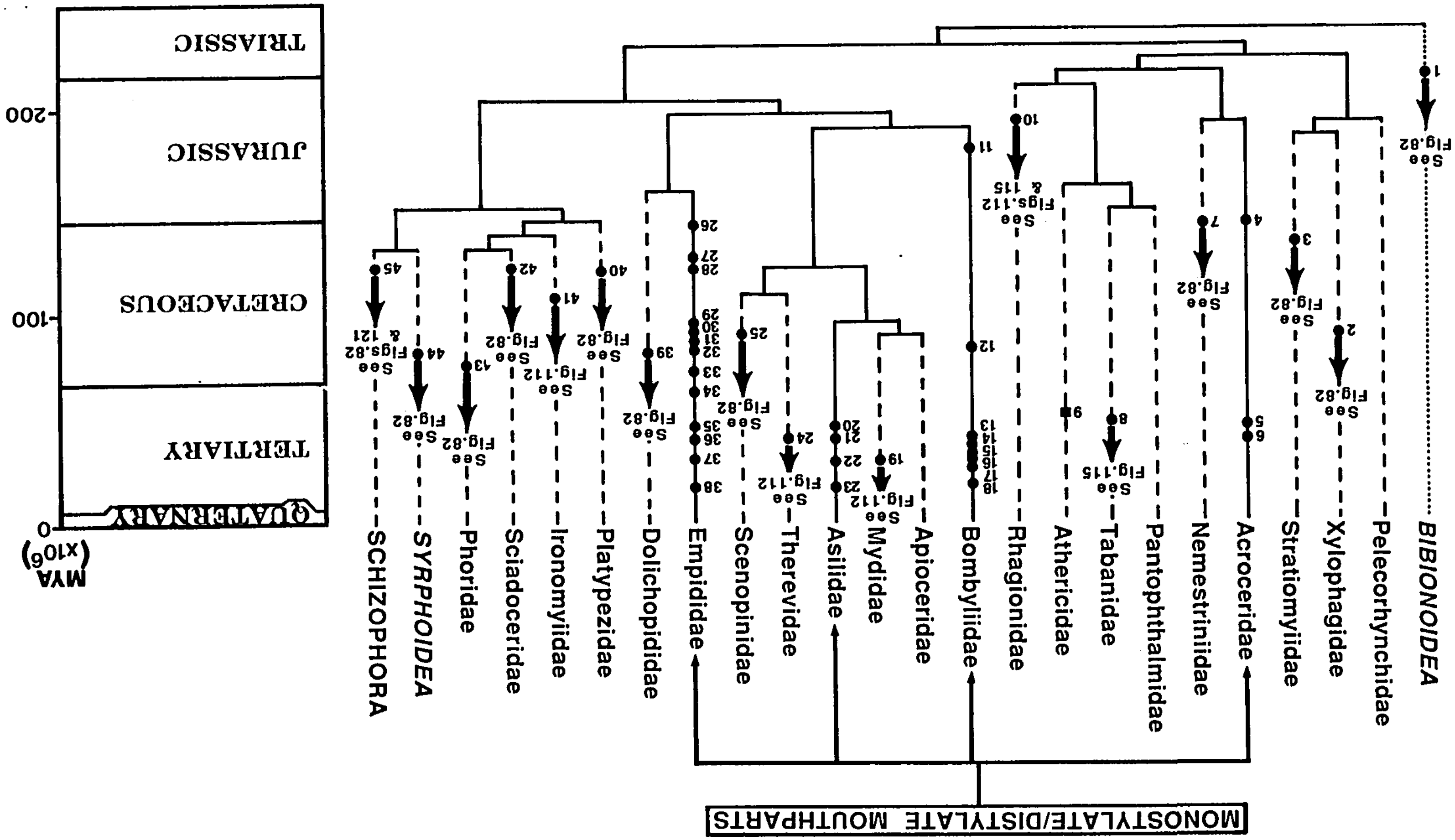
FIGURE 108. Cluster analysis dendrogram of taxa comprising the Monostylae/Distylate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

some empidids supplement their diet with protein and a few are predaceous (Steyskal and Knutson 1981). Predominant members are bombyliids and acrocerids, which have long proboscides that are designed for nectar-probing in flowers. The second theme comprises obligately insectivorous and predaceous forms that are noted for their skill in adroitly capturing prey in flight (Wood 1981).

Geochronologic History. The phylogenetic diversification of monostylate/distylates occurred during a time interval ranging from the Early Jurassic (Bombyliidae) to the Middle Cretaceous (Asilidae), based on fossil evidence and cladistic relationships (Fig. 109). Two trophic groups constitute this diversification--insectivorous forms such as nonhybotine empidids and asilids and nectarivorous forms such as bombyliids, acrocerids and hybotine empidids. The pattern of timing of these two groups is not clear, although there are claims that nectarivores evolved later, during the Late Cretaceous in concert with the evolutionary expansion of angiosperms (Willemstein 1987, Waters 1989a,b).

The earliest presumeably insectivorous monostylate/distylate is the plesiomorphic empidid, *Protempis antennata* Ussatchov 1968, from the Upper Jurassic of the USSR [60] (Waters 1989a,b). Other insectivorous empidids are an unnamed form from the earliest Cretaceous of England [57] (Jarzembowski 1980), an ocydromine from Upper Cretaceous amber of France [45] (Schlüter 1978), an empine from lower Upper Cretaceous deposits of Botswana [43] (Waters 1989a), and a trachydromine from Upper Cretaceous amber of Siberia [37] (Kovalev 1978). The fossil record of

FIGURE 109. Geochronologic history of the Monostylate/Distylate Mouthpart Class. See Appendix F for taxa, localities, and references corresponding to each fossil occurrence. The phylogram is after McAlpine and Martin (1966), Rohdendorf (1980), Hennig (1981), Matile (1981), Woodley (1989) and Waters (1989a, 1989b). The level of taxonomic analysis is the family. The outgroup is Bibionoidea. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.


MYA (x10^6)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
SCHIZOPHORA
SYRPHOIDEA
Phoridae
Sciadoceridae
Ironomyiidae
Platypezidae
Dolichopodidae
Empididae
Scenopinidae
Therevidae
Asilidae
Mydidae
Apioceridae
Bombyliidae
Rhagionidae
Athericidae
Tabanidae
Pantophthalmidae
Nemestriniidae
Acroceridae
Stratiomyidae
Xylophagidae
Pelecorhynchidae
BIBIONOIDEA
See Figs.82 & 121
See Fig.82
See Fig.112
See Figs.112 & 115
See Fig.115
MONOSTYLATE/DISTYLATE MOUTHPARTS
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45

insectivorous empidids becomes qualitatively better during the Tertiary. Although scenopinid asiloids have been documented from the Upper Jurassic of the USSR (Rohdendorf 1974, 1980), the earliest known asilid is from the Late Eocene of the Wyoming [23] (Wilson 1978a).

The fossil history of nectarivorous monostylate/distylates originates with a Middle Jurassic bombyliid from the USSR [65] (Kalugina and Kovalev 1985), although this early taxon may have lacked elongate, nectar-associated mouthparts. The much younger *Proplatypygus*, a bombyliid from Siberian amber [37] however does possess long, nectar-associocited mouthparts (Zaitzev 1981). Several bombyliids have been found in Late Eocene to Late Miocene Dominican amber [17] (Baroni-Urbani and Saunders 1982). The earliest acrocerid, *Archocyrtus gibbosus* Ussatchov 1968, comes from Upper Jurassic deposits of the USSR [60], although this group does not reappear in the fossil record until the Middle Tertiary [23,19] (Hennig 1968, Wilson 1978a). One subfamily of the nominally insectivorous and predaceous Empididae, the Hybotinae, is nectarivorous and is represented by the fossil *Trichinites cretaceous* Hennig 1970 from the Lower Cretaceous amber deposits of Lebanon [55]. This oldest record for a nectarivorous empidid is succeeded by *Pseudacarteus orapensis* Waters 1989b from the Lower Cretaceous of Botswana [43]. Other hybotine empidids are recorded from Early Tertiary deposits. According to Waters (1989b), hybotine empidids were pollinators of Early Cretaceous angiosperms and were subsequently outcompeted by more efficient pollinators during the Late Cretaceous and Early Tertiary.

Previous Designations. In discussions of mouthpart groups prior to the 1930's, the monostylate/distylate mouthpart class was subsumed under a general "dipteran" designation that included several mouthpart classes of this study. Later Metcalf (1929) and Metcalf et al. (1962) considered the "common biting fly or dipterous subtype" as a theme within a piercing-sucking type of their Haustellate Series (Table 6). However none of the four taxonomic families of their members of the monostylate/distylate class were mentioned. James and Harwood (1969), Denis and Bitsch (1973) and Smith (1985) similarly did not indicate that asilids, acrocerids, empidids or bombyliids possessed mouthpart structures different from other dipterans although Matsuda (1965) devoted a discussion to Whitfield's (1925), Bletchley's (1954) and Kristoph's (1961) studies of asilid and empidid mouthparts. Chaudonneret (1989b), in his series of articles on hexapod mouthparts (1983 to 1989b), provided an account of the function and structure of asilid head and mouthpart structure. In general the monostylate/distylate mouthpart class has been regarded as a brachyceran version of typical nematoceran mouthparts.

The mouthpart grouping documented in this section previously has not been named. The designation **monostylate/distylate** is meaningful as a structurally descriptive label and as a reference to the most important, diagnostic mouthpart feature of the group. The term monostylate/distylate has no prior history of usage.

Review of Literature. Important sources for data regarding monostylate/distylate mouthparts originates principally from three studies describing the head and mouthpart structure of several empidids and an asilid, and several monographic accounts detailing mouthpart form and frequently mouthpart evolution within dipterans and their immediate ancestors. However, prior to these works, several authors during the late 1800's and early 1900's presented some of the first descriptions of monostylate/distylate mouthparts. They include Packard (1898) for the asilid *Machimus atricapillus* Fallén, Smith (1898) for *Empis*, *Bombylius* and the asilid *Laphria* and Wesché (1902, 1904, 1909) for *Empis livida* Linneaus, *Asilus crabronformis* Linneaus and the empidid *Tachydromia cursitans* Fabricius. Subsequently several major monographic accounts of mouthpart structure of the Diptera were presented, including Peterson's (1916) exhaustive descriptions of dipteran head and mouthpart structure of the asilid *Promachus vertebratus* and the bombyliid *Exoprosopa fasciata* Macquart, Crampton's (1942) study of external dipteran structure of the acrocerids *Oncodes*, *Lasia* and *Acrocera*, and the asiloid *Astochia*; Snodgrass' (1943, 1944) contributions to piercing-and-sucking dipterans, including a discussion of asilid mouthparts; and Hoyt's (1952) study of the evolution of dipteran mouthpart structure, in which the asilid *Dioctria albius* Walker was viewed as a structural precursor to a generalized stock that gave rise to the bombyliids such as *Toxophora* Osten Sachen. Meanwhile the mouthpart structures of the *M. atricapillus* and the feeding habits of asilids in general were described by Whitfield (1925), the head and mouthpart structures of *Empis livida* Linneaus by Bletchley (1954), and descriptions of mouthpart features of several empidids were given by Krystoph (1961). Recent taxonomic and natural-historical accounts of monostylates/distylates can be found by a multiauthored monograph on Nearctic dipterans (McAlpine 1981), including chapters on asilids (Wood 1981c), acrocerids (Schlinger 1981), bombyliids (Hall 1981) and empidids (Steyskal and Knutson 1981).

8.9.6. Distylate/Tetrastylate Class (Class 28)

Description. Head quadrate; proboscis short, rarely long. Genae and gula prominent to minimally developed. Antennae stylate or less commonly otherwise; ocelli 3; compound eyes variable. Mouthparts hypognathous, retractile, labellate, with 2 or 4 stylets.

Clypeal shape variable, fused to frons. Labrum transversely elongate or quadrate, undivided, with a variable margin. Hypopharynx long and stylate, rarely otherwise; epipharynx stylate and adjoined to labrum, rarely otherwise. Mandibles absent. Maxilla with one basal sclerite and bearing a lacinia and palpus only. Maxillary palpus variable in type, segmentation and length; lacinia stylate-acuminate, long. Labium with one or two basal sclerites, bearing a labellum and with or without glossae. Labial palps 2-segmented, labellate and short. Glossae generally absent; when present lingulate or papillate.

Key Phenocharacters. Distylate/tetrastylates bear the unique combination of a short, retractile, hypognathous labellum bearing a distal fleshy expansion, and either hypopharyngeal and epipharyngeal stylets in combination with a pair of lacinial stylets (the tetrastylate condition) or a pair of lacinial stylets only (the distylate condition). The distylate/tetrastylate mouthpart class is one of several stylate-haustellate mouthpart types with an overall dipteran facies and thus must be distinguished from the monostylate/distylate, hexastylate, tubulostylate and labellate classes. Distylate/tetrastylates cannot be confused with other, nondipteran mouthpart classes.

Distylate/tetrastylates most closely resemble monostylate/distylates (Section 8.9.5), but are differentiated from them by presence of a short, distally-expanded proboscis and presence of an epipharyngeal stylet in almost all forms. When compared to hexastylates (Section 8.9.7), distylate/tetrastylates have two or four stylets rather than six stylets and the presence of a stout, brachyceran labellum rather than the longer, nematoceran labellum. Unlike the distylate/tetrastylate condition, tubulostylates possess a prognathous, often dorsoventrally flattened head with prognathous mouthparts consisting of a single stylet formed from a modified, rigid labellum with prestomal teeth (Section 8.9.9). Labellate mouthparts (Section 8.5.3) lack stylets, although the labellum (modified labial palps) is near indistinguishable in both classes.

Diversity and Natural History. The distylate/tetrastylate mouthpart class comprises fluid-feeding, insectivorous or nectarivorous, medium- to very large brachyceran dipterans (Fig. 110) that are strong fliers and runners and occur in a variety of terrestrial habitats. Two major trophic groups are clearly differentiable: (i) insectivores that feed by sucking out liquified contents of insectan prey, and (ii) nectarivores and (exposed?) plant sap-feeders on vascular plants. The major ecologic competition for distylate/tetrastylates originates from other dipteran mouthpart classes, specifically monostylate/distylates,

CLASS 28: DISTYLATE/TETRASTYLATE

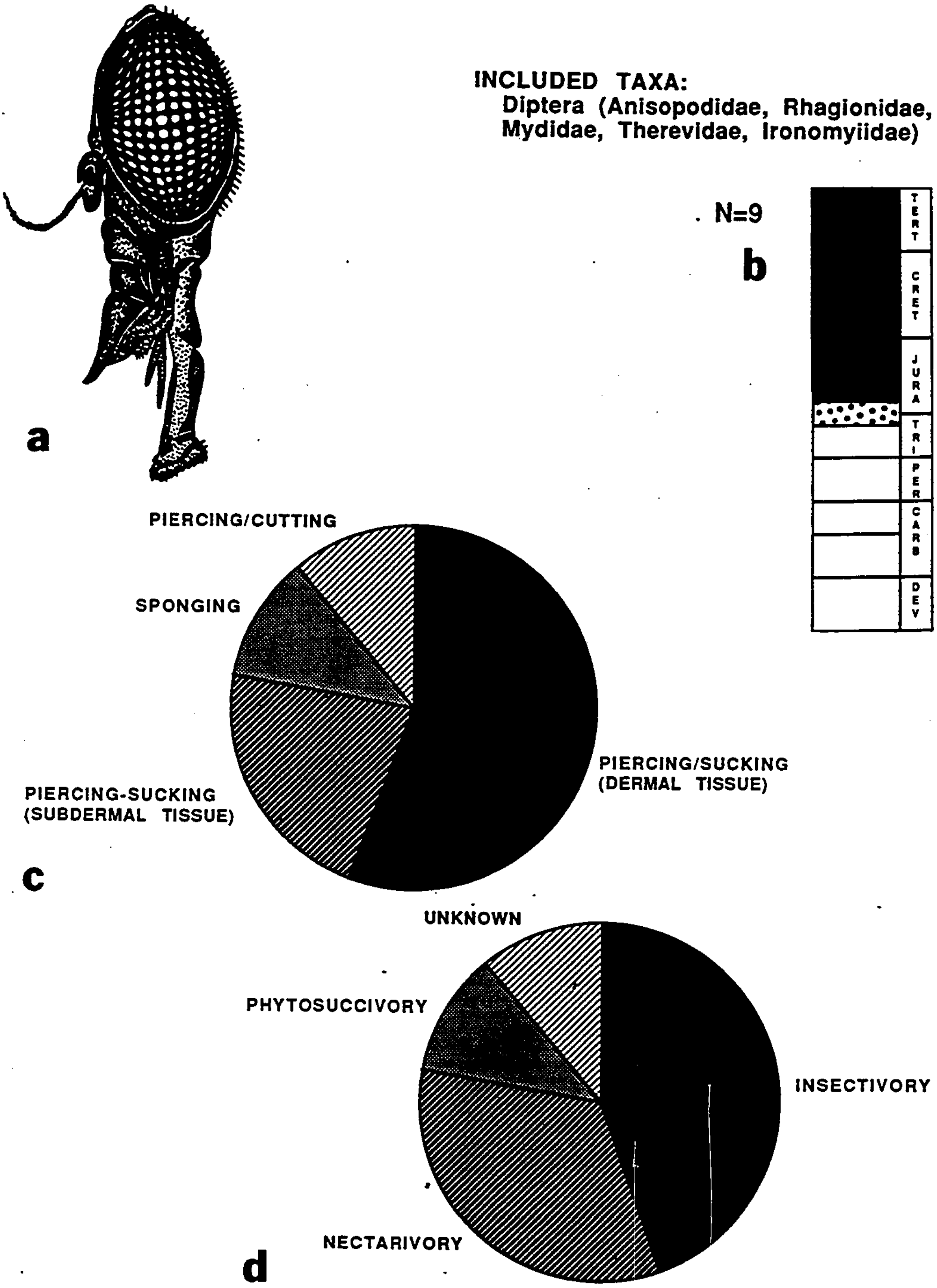


FIGURE 110. Overview of the Distylate/Tetrastylate Mouthpart Class. a, *Ironomyia nigromaculata* White (Diptera: Ironomyiidae, data-set no. 921); b, taxonomic distribution, numbers of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

some hexastylates and probably labellates; distylate/tetrastylates probably do not compete with faithful pollinators such as glossates or siphonates. The distylate/tetrastylate class taxonomically comprises five families and approximately 60 genera and 1100 species (Appendix D), translating to a rank-order of 26 out of 34 mouthpart classes (Table 5, Fig. 131). Although the origin of the mouthpart class can be traced to the Late Triassic, they currently do not comprise a significant proportion of extant insect diversity.

Therevid, mydid and rhagionid members of the mouthpart class consist of both insectivorous and plant-imbibing species--a distinction which is often gender-specific. Females tend to be predatory and insectivorous whereas males are generally nectarivorous or imbibe plant sap. Although some therevids are predaceous, most are fluid-imbibers of nectar, sap, exudates, honeydew and various insect secretions (Irwin and Lyneborg 1981) and are associated with flowers (Proctor and Yeo 1973). Mydids are similarly flower-feeders (Wilcox 1981, Zaitlin and Larsen 1984), although some with atrophied mouthparts probably do not feed and others may be predatory (Parmonov 1950). Anisopodids apparently only feed on nectar and other fluid foods (Malloch 1917). Whereas most female rhagionids are predaceous on other insects (Richards and Davies 1977, Willemstein 1987), most males and a few females feed on honeydew and plant fluids, including nectar (James and Turner 1981). Other rhagionids such as *Symphoromyia* suck blood of warm-blooded vertebraes and are hexastylates. The dietary and feeding habits of ironomyiids are unknown.

Structural Themes. Five characters distinguish the two themes that are expressed in the dendrogram of distylate/tetrastylate mouthpart (Fig. 111). The first theme consists of three anisopodid taxa (Subcluster 1, data-set taxa 852 to 853 in Fig. 111), and is characterized by the presence of a nematoceran-aspect fasiculate haustellum, nonstylate or nonaristate antennae, a conspicuous clypeal pump, a quadrate-shaped labrum, a maxillary palp with an enlarged middle segment and lingulate glossae. The second theme consists of the remaining taxa (Subcluster 2, taxa 875 to 904) which bear a brachyceran-aspect, labellate haustellum, stylate or aristate antennae, a de-emphasized clypeal pump, a transversely-elongate labrum, more generalized maxillary palpi without enlarged middle segments and either rudimentary glossae or glossal absence. These two themes are not significant departures from the many characters that define distylate/tetrastylate mouthparts (see branch-lengths of clusters in Fig. 28) and should be regarded as only minor patterns.

Geochronologic History. The geochronologic history of the distylate/tetrastylate mouthpart class is characterized by the loss of two or four paired or unpaired stylets from the six-stylet condition that occurred plesiomorphically in hexastylates (see Section 8.9.7). The pattern of distylate/tetrastylate diversification is characterized by initial establishment of an early nematoceran (anisopodan) lineage by Late Triassic time, followed soon thereafter by a brachyceran (rhagionid) lineage during the Early Jurassic and subsequent evolution of the more apomorphic Mydidae and Therevidae probably during the Early

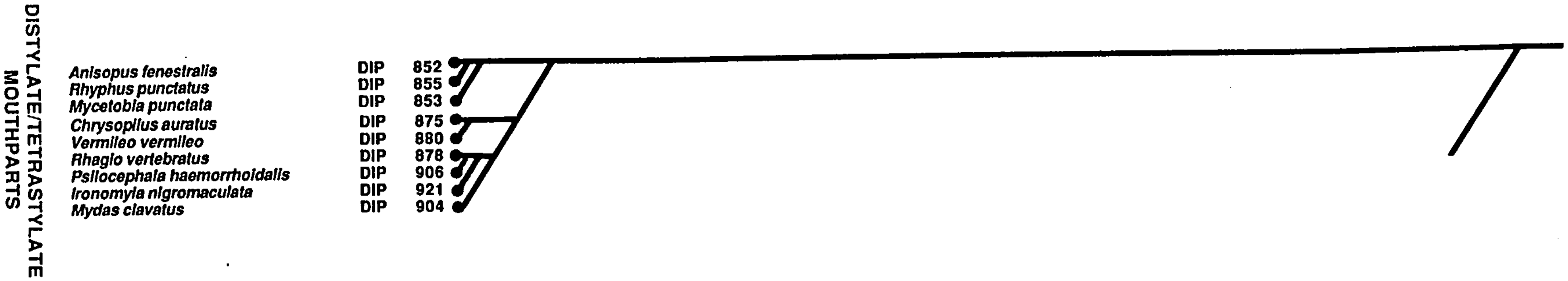
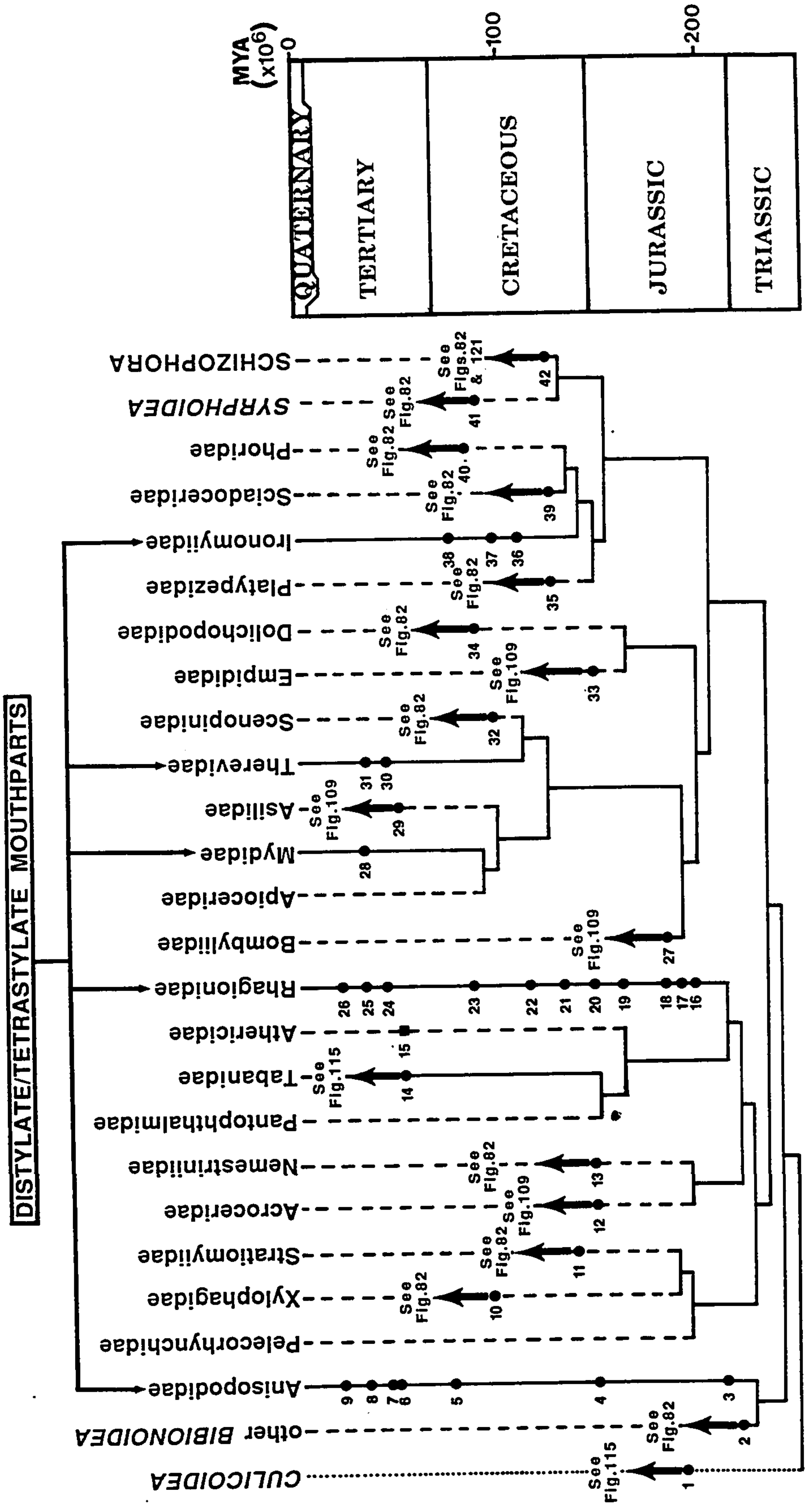

DISTYLATE/TETRASTYLATE MOUTHPARTS
Anisopus fenestralis DIP 852
Rhyphus punctatus DIP 855
Mycetobia punctata DIP 853
Chrysopilus auratus DIP 875
Vermileo vermileo DIP 880
Rhagio vertebratus DIP 878
Psilocephala haemorrhoidalis DIP 906
Ironomyia nigromaculata DIP 921
Mydas clavatus DIP 904

FIGURE 111. Cluster analysis dendrogram of taxa comprising the Distylate/Tetrastylate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

Cretaceous (Fig. 112) (after Rohdendorf 1974, 1980; Kalugina and Kovalev 1985). The Ironomyiidae, apparently a plesiomorphic cyclorrhaphan group, probably has a more ancient ancestry and may have originated during the Late Jurassic or Early Cretaceous (McAlpine and Martin 1966). It is highly likely that members of any one of these clades became attracted to nectar as a food during the Cretaceous angiosperm diversification (Willemstein 1987) or even earlier.

The Anisopodidae is the earliest-occurring distylate/tetrastylate clade, with *Protolbiogaster rhaetica* Kalugina 1985 from the Late Triassic/Early Jurassic of the USSR [73] referrable to the family. The anisopodid fossil record is only moderately represented; younger occurrences include taxa from the Upper Jurassic of the USSR [60] (Rasnitsyn 1988), Upper Cretaceous of Canada [35] (McAlpine and Martin 1969) and various Tertiary records [23,19,15] (Wilson 1978a, Keilbach 1982). The earliest rhagionid is *Protobrachyceron liasinum* Handlirsch 1908 from the Early Jurassic of Germany [68]; an approximately coeval species is *Ija problematica* Kovalev 1981 that has been documented from the USSR [67]. A relatively rich fossil record of rhagionids is known from the Jurassic [68-65,62,60] (Kovalev 1981, 1982, 1985; Kalugina and Kovalev 1985) although it becomes sparser during the Lower Cretaceous with occurrences in strata from England [57] (Jarzembowski 1984) and southern Australia [53] (Jell and Duncan 1986). Ambers from the Upper Cretaceous of the USSR [37] (Zherikin and Sukacheva 1973) and the Upper Eocene/Lower Oligocene of the Baltic Region [19] (Hennig 1967) as well as other Tertiary occurrences contain well documented rhagionids (Fig.

FIGURE 112. Geochronologic history of the Distylate/Tetrastylate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after McAlpine and Martin (1966), Rohdendorf (1980), Hennig (1981), Matile (1981), Woodley (1989) and Waters (1989a, 1989b). The taxonomic level of analysis is the family. The outgroup is Culicoidea. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.


CULICOIDEA
other BIBIONOIDEA
Anisopodidae
Pelecorhynchidae
Xylophagidae
Stratiomyidae
Acroceridae
Nemestriniidae
Pantophthalmidae
Tabanidae
Athericidae
Rhagionidae
Bombyliidae
Apioceridae
Mydidae
Asilidae
Therevidae
Scenopinidae
Empididae
Dolichopodidae
Platypezidae
Ironomyiidae
Sciadoceridae
Phoridae
SYRPHOIDEA
SCHIZOPHORA
DISTYLATE/TETRASTYLATE MOUTHPARTS
See Fig.115
See Fig.82
See Fig.109
See Figs.82 & 121
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42
MYA ($\times 10^6$)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC

112). The Ironomyiidae, first recognized in the Recent fauna by a rare southern Australian and Tasmanian species (McAlpine and Martin 1966) has now been recognized in Upper Cretaceous amber from Canada [35] by McAlpine (1973), although ironomyiids subsequently have been recorded from older Cretaceous sediments [52,42] (Rasnitsyn 1988). Mydids and therevids have poor fossil records; both are known from the Early Oligocene of Colorado [15] (Cockerell 1909, 1913), although a therevid has been documented from older Baltic amber [19] (Keilbach 1982).

Previous Designations. This mouthpart type has not been discussed or recognized previously as a discrete structural type, with the possible exception of references to a tabanoid brachyceran mouthpart type (Denis and Bitsch 1973, Smith 1985, Chaudonneret 1989b). In these examples the mouthpart structure of the hexastylate, *Tabanus*, was described as a model for a mouthpart type, which is not applicable to the distylate/tetrastylate condition described herein. (See Table 6 for a brief history of nomenclature.) I am using the term **distylate/ tetrastylate** to refer to the mouthpart class of this section because of the presence of either two or four-stylets as the principal, interactive mouthpart elements.

Review of Literature. The structure of distylate/tetrastylate mouthparts is well-documented in several comprehensive studies of the mouthparts from several selected species, numerous partial accounts describing mouthpart elements and a few major surveys of mouthpart structure throughout the order. Major accounts devoted to distylate/ tetrastylate mouthpart structure include Bletchley (1955) for the rhagionid *Rhagio scolopacea* (Linneaus), Chassagnard and Tsacas (1974) for the rhagionids *Chrysopilus auratus* Fabricius and *Vermileo vermileo* DeGeer, and Zaitlin and Larsen (1984) for the mydid *Mydas clavatus* (Drury). Various examinations of selected distylate/tetrastylate mouthpart structures include Kellogg (1899) for the anisopodid *Rhyphus* sp., Wesché (1909) for *C. auratus*, Anthon (1943a) for details of anisopodid mouthparts, McAlpine (1967) for the ironomyid *Ironomyia* White, Teskey (1981c) for *V. vermileo*, Peterson (1981a) for the anisopodid *Mycetobia divergens* Walker, and Wilcox (1981) for *M. clavatus*. The last three of these sources are found in volume 1 of *Manual of Nearctic Diptera*, edited by McAlpine et al. (1981). Lastly, valuable references for mouthpart and head structure of several taxa of distylate/tetrastylates can be found in Peterson (1916), Crampton (1942) and Hoyt (1952).

8.9.7. Hexastylate Class
(Class 29)

Description. Head quadrate or vertically prolonged; proboscis short to very long. Genae minimally developed to expansive; gula minimally- to well-developed. Antennae setaceous, filiform, moniliform, plumose or stylate; ocelli absent, rarely 2 or 3; compound eyes expansive or rarely divided into separate units. Mouthparts hypognathous, stylate-haustellate, hexastylate (very rarely tetrastylate), nonretractile. Food pump clypeal and pharyngeal.

Clypeus quadrate, infrequently vertically-elongate; fused to frons or undivided and separate. Labrum vertically very elongate, rarely transversely-elongate; undivided; margin spinose, mucronate/acuminate or acute. Hypopharynx long and stylate, with a salivary syringe; epipharynx stylate, adjoined to labrum. Mandibles monocondylic; stylate or ensiform blades; serrated, rarely edentate; musculated by protraction/retraction. Maxillary basal sclerites variable in shape and number; infrequently lacking a galea. Maxil lary palps pectinate, filiform-clavate or serrate; intermediate to rarely long in length. Galea mostly absent, rarely a generalized lobe; lacinia stylate-acuminate. Labium basal segments variable in shape and number; paraglossae absent, glossae often absent. Labial palpus a 2-segmented labellum. Glossae generalized, papillate, penicillate or infrequently absent. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. The distinctive feature of the Hexastylate Mouthpart Class is the presence of haustellate mouthparts bearing six stylets and the lack of a lever-based protraction/retraction mechanism for the proboscis. Important features that are associated but not diagnostic of hexastylates when compared to other adult dipteran mouthpart classes include the lack of ocelli and the presence of serrated, ensiform or stylate mandibles.

Adults of noncyclorrhaphan dipterans are members of four mouthpart classes, namely the labellate, monostylate/distylate, distylate/tetrastylate and hexastylate classes (Sections 8.5.2, 8.9.5 to 8.9.7). There is significant taxonomic overlap among these mouthpart classes. While labellates lack stylets, the other three are differentiated primarily by stylet number. Hexastylates possess the full complement of epipharyngeal, hypopharyngeal, paired mandibular and paired lacinial stylets; monostylate/distylates either have a single hypopharyngeal stylet or paired lacinial stylets; and distylate/tetrastylates bear either two (paired) lacinial stylets, or four stylets consisting of a hypopharynx, epipharynx and paired laciniae (see Sections 8.9.5 and 8.9.6). Also, hexastylates are separated from the other noncyclorrhaphan mouthpart classes by the presence of prominent, piercing or cutting mandibles that the others lack. Confusion with the Segmented Beak Mouthpart Class (Section 8.9.2) is avoided by recognition of differences in stylet number and the complete absence of palpi in segmented beaks. Some taxa in the nonhaustellate mouthpart classes (Sections 8.8.2, 8.8.3) bear six stylets, but they lack a haustellum and possess major differences in palpal presence and type.

Diversity and Natural History. Hexastylates comprise small- to medium-sized, able-flying insects that are predaceous on other insects, sanguinivorous (blood-sucking) on terrestrial vertebrates and infrequently nectarivorous on flowering plants (Fig. 113). In terms of their effect as predators on insects and tetrapod vertebrates and their underappreciated, modest role as pollinators of flowering plants, hexastylates are a moderately important component in terrestrial ecosystems. Hexastylates comprise 10 families, 400 genera and approximately 14,600 species (Appendix D) and have a rank-order of 13 out of 34 mouthpart classes (Table 5, Fig. 131). Based on certain assumptions of character-state reversals, the origin of hexastylate mouthparts may have occurred only once, with concomitant reduction of stylets and corresponding

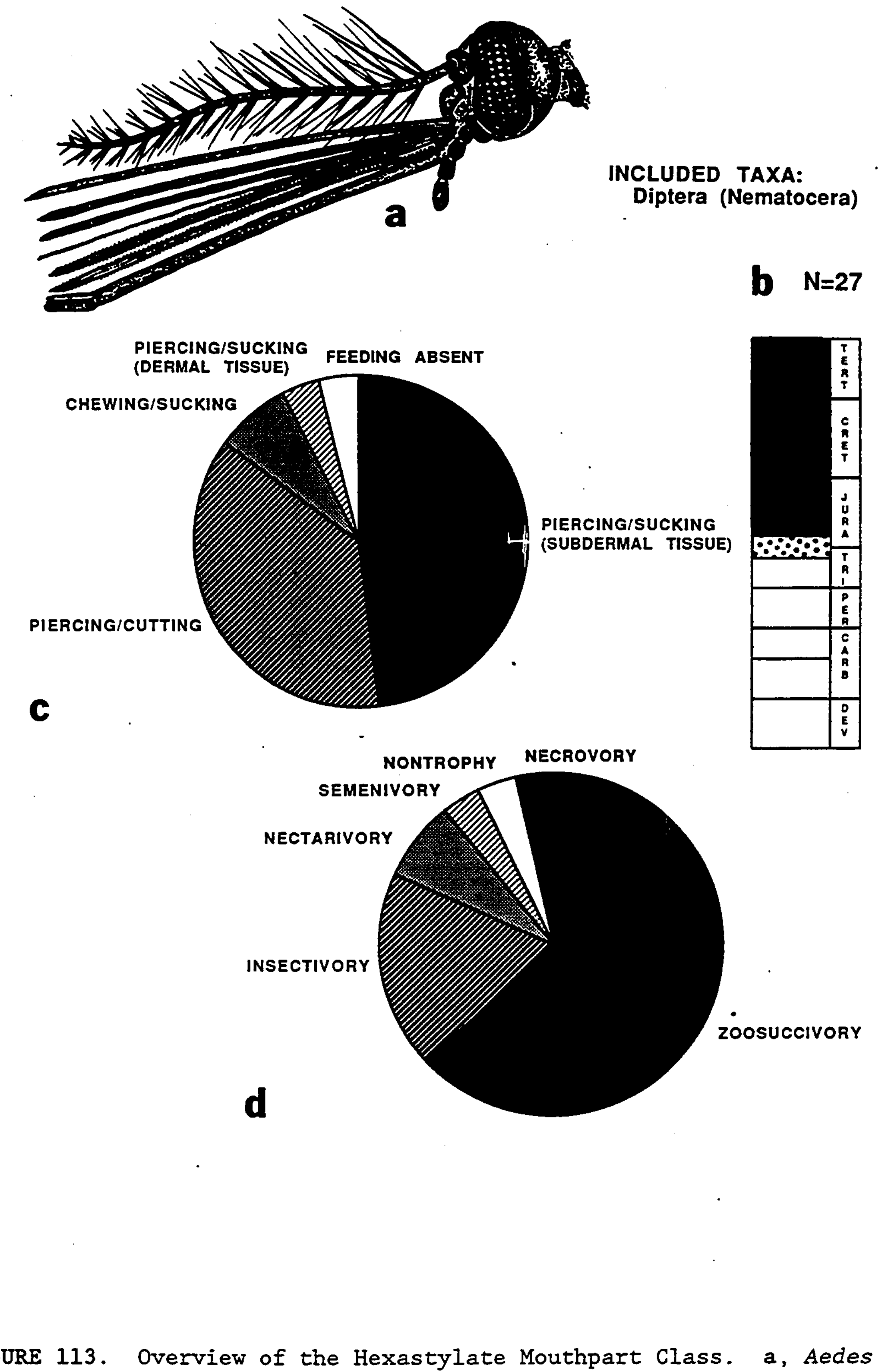


FIGURE 113. Overview of the Hexastylate Mouthpart Class. a, *Aedes aegypti* (Linneaus) (Diptera: Culicidae, data-set no. 821); b, taxonomic distribution, numbers of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

expansion of the labellar surface in several clades (Downes 1971, the hypothesis preferred herein), or it may have originated as many as four times (Psychodidae, Culicoidea, Belepharoceridae, Tabanidae + Rhagionidae), if the ancestral dipteran was labellate. There is limited evidence that the hexastylate condition is diphyletic, originating once in primitive Nematocera and again in the primitively labellate Brachycera (see Mattingly 1965, Downes 1971). Recent paleobiological evidence indicates that hexastylates extend to the Triassic and possibly the Permian (Downes 1971, Rohdendorf 1974).

There is substantial documentation of the feeding mechanisms, diets and general ecology of hexastylates. Much of this descriptive data originates from various investigations of pathogen-transmitting dipteran species in tropical and subtropical regions. Motivation for understanding the feeding habits, diets and hosts of many hexastylate species involve attempts toward their biological control and, in some cases, eradication of disease vectors in regions of pandemic infestation. All sanguinivorous hexastylates are predatory on mammals, birds, reptiles, amphibians and amphibious fish, in decreasing order of frequency. A few, such as the culicid *Toxorhynchites* may be entirely nectarivorous (Gillett 1971). Although various nectar-containing sugars are important for most species as a food source, less is known about nectarivory than sanguinivory (O'Meara 1987).

Hexastylates have a distinctive feeding cycle that may be either nocturnal or diurnal since sanguinivory and nectarivory is confined to a few hours or less per day (O'Meara 1987). Consequently, vertebrates must be spatially and temporally available during these feeding hours if feeding is to occur. Thus, in many predators studied, host-locating behavior is important and includes senses capable of monitoring host attributes such as temperature, odor, movement and, infrequently, sound (O'Meara 1987). Once the hexastylate predator has approached the host other types of sensory organs are engaged that are capable of detecting carbon dioxide and heat production, humidity and light intensity of a potential host (McIver and Sutcliffe 1986). After alighting on a suitable host, feeding generally commences. The frequency of feeding varies considerably within hexastylates. Some species from all constituent taxonomic families are autogenous (the derived condition) and thus are able to oviposit their first batch of eggs without a blood meal, whereas anautogenic species require one or two blood meals for ovigenesis (Downes 1971). Overwintering forms may require several blood meals for the production of fat bodies that are subsequently metabolized for ovigenesis and oviposition during the ensuing Spring. For anautogenous forms, evidence indicates that a minimum volume of blood is necessary to induce the gonotrophic cycle; for those lacking a gonotrophic cycle, feeding occurs more requently and can be as often as 12 times per day in tabanids but more commonly is twice daily. Most forms feed once every three to ten days (O'Meara 1987). For other anautogenous forms blood alone is insufficient for ovarian development and carbohydrates are required for the production of fat bodies for metabolism after the first gonotrophic cycle (Downes 1958). In laboratory experiments females that were blood-fed died in two weeks whereas females that were fed on blood and sugar lived for 12 weeks (Leeson 1939). Apparently amino acids from blood contain a protein that is essential for egg development.

Most accounts of dipteran evolution conclude that insectivory is plesiomorphic and sanguinivory is apomorphic (Beklemshev 1957, Downes 1958, Waage 1979, Jones 1989). The principal hypothesis for the origin of sanguinivory posits a transformation series in which a predaceous ancestral nematoceran fed on other nematocerans, particularly blood-unengorged culicids. This predator eventually shifted to predation on culicids with distended abdomens of mammalian blood and was followed later by direct predation on mammalian hosts. This hypothesis begs the question of the ultimate origin of sanguinivory; an alternative hypothesis suggests that predation on mammalian host blood is ancestral and both consumption of "secondhand" mammalian blood from engorged culicids and predation on other nematocerans are derived (Downes 1958).

Although there are many hexastylate taxa that are predaceous on other insects and suck out their bodily fluids for food, most are sanguinivorous (Fig. 113). Sanguinivory has assumed two major feeding strategies. The first strategy are those taxa, such as Culicidae (mosquitoes) and Chaoboridae (phantom midges), with long proboscides that locate individual subdermal capillaries and insert their stylet tube some distance into the blood vessel lumen for imbibation (Downes 1971). The second feeding strategy occurs in other taxa such as Ceratopogonidae (punkies), Simuliidae (black flies) and Tabanidae (horse flies) that bear bladelike, slashing mandibles and laciniae instead of long, gracile, piercing stylets and are able to lacerate surface skin for imbibation of the resulting pooled blood (Downes 1971). A "transitional" feeding style occurs among some culicids that are able to locate a subdermal capillary with their stylet fasicle but are unable to penetrate the vessel lumen after it has been punctured (Gillett 1971). As the capillary blood hemorrhages and pools in the surrounding tissue, it is imbibed. Further subdivisions of feeding type can be made within the two above feeding strategies. Gad (1951) has characterized the structurally diverse, bladelike mouthparts of ceratopogonids into types that are associated with nectarivory, sanguinivory and insectivory.

Insectivory is common in most hexastylate families and particularly among ceratopogonids. Predaceous ceratopogonids generally capture prey in flight by use of raptorial legs and hooked tarsal claws, frequently tumbling to the ground after the prey is captured. The victim is punctured in the eye, neck or other membranous region, and the liquified body tissues of the prey is sucked dry after proteinase-laden saliva is injected into the victim. Virtually all insect orders are attacked by ceratopogonids, including comparatively large, ground-dwelling orthopterans (Gad 1951), but especially other dipterans. Ceratopogonid genera such as *Forcipomyia* common feed on large blood vessels of the wings of large insects such as dragonflys, butterflys and planipennians (Gad 1951, Downes 1971). Individuals of the same genus have been recorded sucking the body fluids from a caterpillar for a few days until the victim died and ovarian development of the predator was complete, indicating a rare example of hexastylate parasitism (Downes 1971). Females of the ceratopogonid *Atrichopogon* sp. attack meloid and oedomerid beetles by puncturing their intersegmental membrane (Downes 1955).

The curious habit of female ceratopogonids feeding on conspecific males *in copulo* has been documented by Downes (1978). Female ceratopogonids enter swarms of male conspecifics and during copulation puncture the male in the cervical region for feeding. As the female abdomen is distended from consumption of the male, sperm transfer continues and is later followed by the breaking off of the attached, dry cuticular carcass of the still-attached male. The terminal abdominal segments and attached genitalia of the male often remains attached to the female.

Sanguinivory in hexastylates only occurs among females and is often necessary for ovarian development. Psychodids (moth flies), culicids, chaoborids, simuliids, ceratopogonids, tabanids and rhagionids (snipe flies) are known to attack tetrapods for blood (Williams and Edman 1968, Downes 1971). Although it was once thought that only warm-blooded vertebrates were attacked, substantial evidence now indicates that reptiles, amphibians and even amphibious fish are commonly attacked (Downes 1958, 1971). For example many species are host-specific to or predominately attack frogs, including the psychodid *Syncorax* sp., the culicid *Culex apicalis*, the ceratopogonid *Lasiohelea velox* (Winnertz) and the rhagionid *Atrichops crassipes* (Meigen). Other examples of predation on cold-blooded hosts include the ceratopogonid *Culicoides piliferus* Root and Hoffman on turtles, some species of *Tabanus* that attack crocodiles, lizards and turtles, and the psychodid *Phlebotomus schwetzi* Adler, Theodor and Parrott which feeds on various reptiles. Some species of *Phlebotomus* often have a wide range of hosts, often including reptiles, birds and diverse mammals (Downes 1958). Typical host-associated genera on mammals such as *Aedes*, *Anopheles* and *Culex* have species that feed only on reptiles (Downes 1971). In spite of all the above host occurrences, most hexastylate families attack warm-blooded vertebrates. There is now evidence that the chaoborid *Corethella* and some chironomids (midges) are sanguinivores on vertebrates (Williams and Edman 1968, Downes 1971).

Nectar and pollen recently has been demonstrated as a significant diet in both sexes of some hexastylates. Among culicids many taxa pollinate small, tubular flowers with partially concealed nectar (Lamiaceae, Apiaceae) or large, dish-shaped flowers with accessible nectar (Rosaceae) (Porsch 1958, Proctor and Yeo 1973). There are several records indicating that psychodids and ceratopogonids are attracted to sapromyophilous, heat-producing flowers such as *Aristolochia*, *Arum* and *Cetopegia* (Aristolochiaceae, Araceae) whereas simuliids are attracted to *Salix* (Saliaceae), *Malus* (Rosaceae) and *Hedera* (Araliaceae) (Proctor and Yeo 1973, Faegri and van der Pijl 1980). Specific associations include the pollination of orchids by the culicid *Aedes* in Canada (Gillett 1971) and *Culex* in Australia (Armstrong 1979), pollination of European Asteraceae and *Sambucus* (Caprifoliaceae) by the blepharocerids (net-winged midges) *Apistomyia elegans* Bigot and *Liponeura cinerascens* Loew (Porsch 1958), pollination of North American *Vaccinium* (Ericaceae) by *Simulium damnosum* Say (Downes 1958) and pollination of Apiaceae by the female ceratopogonid *Schizohelea leucopezia* Meigen (Gad 1951). Examples of hexastylate consumption of other carbohydrate sources include extrafloral nectaries, honeydew, exposed plant sap and ripe fruit (Gad 1951; Downes 1958, 1971). Downes (1955) documented the first example of pollinivory among hexastylates in both sexes of the ceratopogonid *Atrichopogon pollinivorous* Downes. This species consumes the pollen grain contents by slicing the grain externally by mandibular stylets and then sucking out the contents, akin to the punch-and-sucking technique of the mouthcones (Section 8.9.4). Since Downes' (1955) discovery, three other species of *Atrichopogon* are presumed to be pollinivorous.

Structural Themes. Six major themes within the hexastylate mouthpart class are evident in Fig. 114. The first theme is a blepharocerid-dominated subcluster comprising three blepharocerids, two psychodids and an ceratopogonid (Subcluster 1, data-set taxa 812 to 869 of Fig. 114). The second theme comprises a culicid-dominated subcluster (816 to 819) with five culicids, a dixid and a chaoborid. A third theme is a ceratopogonid-dominated subcluster (837 to 844), with also a simuliid. The fourth theme is the single psychodid *Psychoda albipennis* Zetterstedt (814). The fifth theme is a brachyceran, tabanid-dominated subcluster (879 to 890) that includes a rhagionid. The sixth theme consists of two simuliids (833, 835). These six subclusters each center on particular family-level groupings, namely culicids, ceratopogonids, tabanids and simuliids. However there is sufficient taxonomic overlap to suggest that many of these themes may be related to features such as mouthpart sexual dimorphism, whether a mandibular piercing-and-sucking or slash-and-cutting method of feeding has been adopted, or whether the distal labellar surface is fleshy or not.

These six themes are largely differentiated by eight characters. Head and general mouthpart-related characters include whether the head is quadrate or vertically-prolonged, whether the proboscis is short,

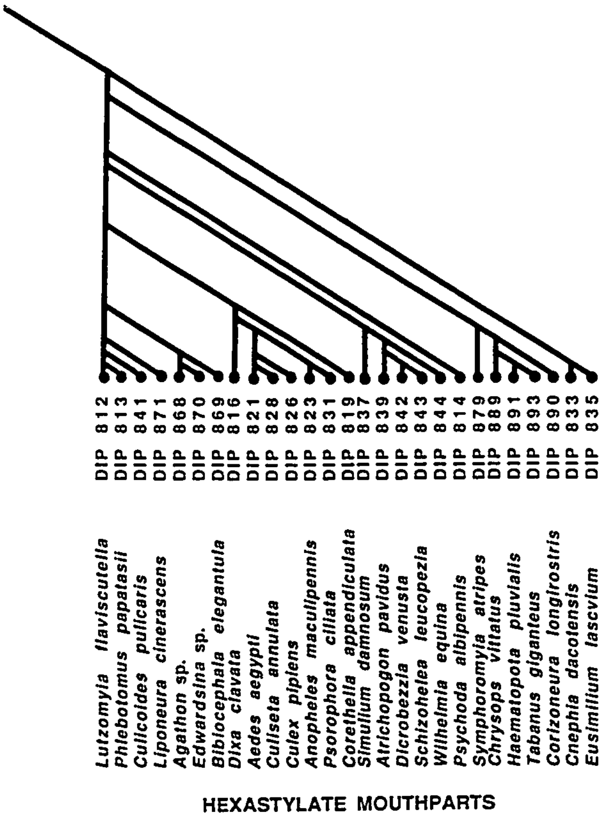

DIP 812 Lutzomyia flaviscutella
DIP 813 Phlebotomus papatasii
DIP 841 Culicoides pulicaris
DIP 871 Liponeura cinerascens
DIP 868 Agathon sp.
DIP 870 Edwardsina sp.
DIP 869 Bibiocephala elegantula
DIP 816 Dixa clavata
DIP 821 Aedes aegypti
DIP 828 Culiseta annulata
DIP 826 Culex pipiens
DIP 823 Anopheles maculipennis
DIP 831 Psorophora ciliata
DIP 819 Corethella appendiculata
DIP 837 Simulium damnosum
DIP 839 Atrichopogon pavidus
DIP 842 Dicrobezzia venusta
DIP 843 Schizohelea leucopezia
DIP 844 Wilhelmia equina
DIP 814 Psychoda albipennis
DIP 879 Symphoromyia atripes
DIP 889 Chrysops vittatus
DIP 891 Haematopota pluvialis
DIP 893 Tabanus giganteus
DIP 890 Corizoneura longirostris
DIP 833 Cnephia dacotensis
DIP 835 Eusimilium lascvium
HEXASTYLATE MOUTHPARTS

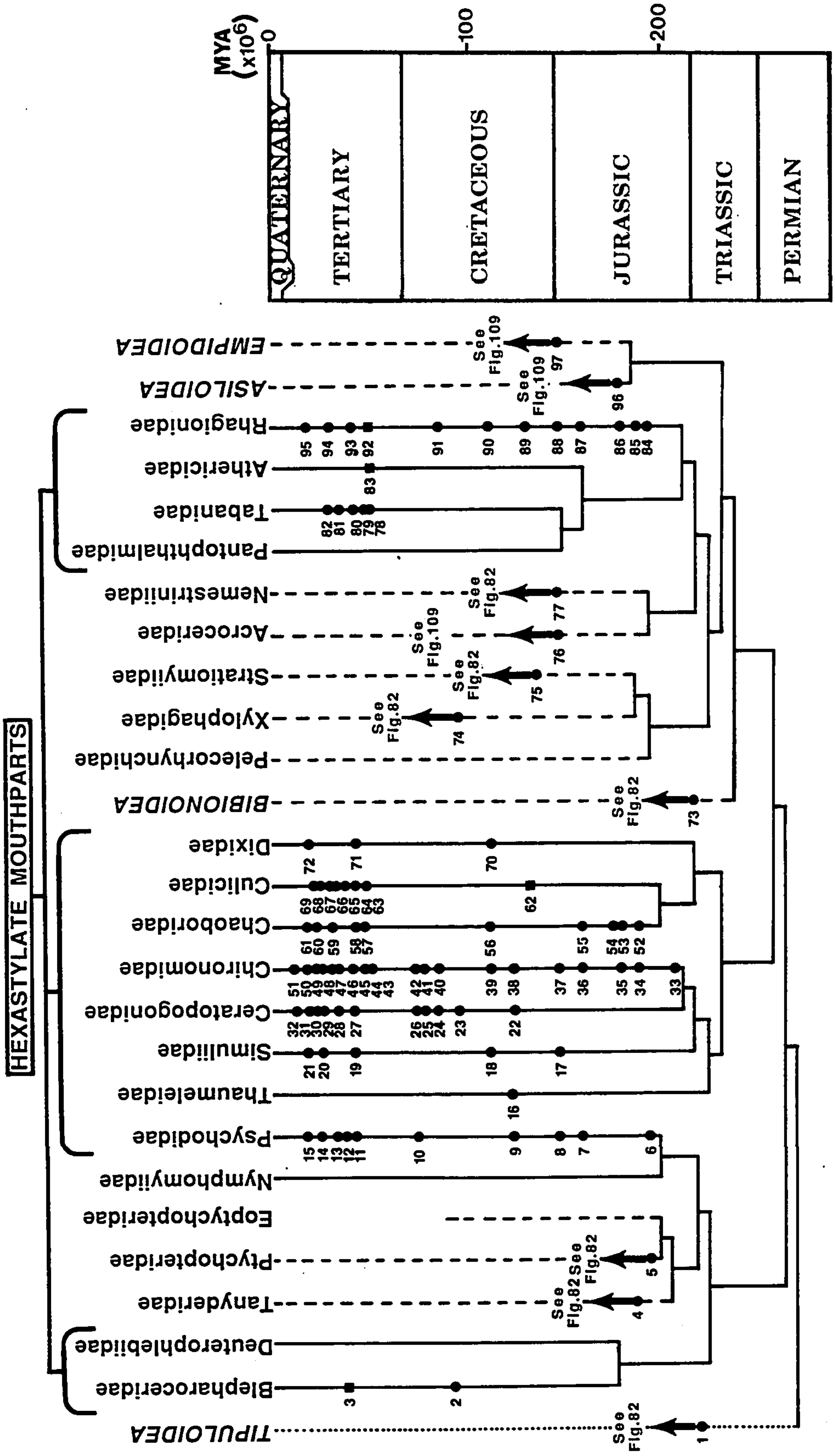
FIGURE 114. Cluster analysis dendrogram of taxa comprising the Hexastylate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

long, or very long, and whether the food pump is dominated by a clypeal or a pharyngeal pump. Specific characters pertaining to mouthparts include whether the labral margin is spinose, mucronate or (rarely) spatulate; whether the mandibles are long and piercing or bladelike and slashing; whether the maxillary palps are filiform-clavate, serrate or pectinate; whether the galea is absent or present as a small generalized lobe; and whether the glossa is absent, vestigial and papillate, or larger and generalized. Some of these characters, particularly proboscis length, mandibular type and nature of the food pump are associated with distinctive feeding styles.

Each of these six themes were discussed and recognized by Matsuda (1965), Smith (1985) and Chaudonneret (1989b) in their reviews of piercing-and-sucking mouthparts in dipterans. The established the mouthpart distinctiveness of culicids (theme 2 above), psychodids/ ceratopogonids (themes 1, 3 and 4), simuliids (theme 6) and horse flies (theme 5). Denis and Bitsch (1973) and to a lesser degree Snodgrass (1943) additionally recognized mouthpart structure and distinctions among blepharocerids, psychodids and ceratopogonids (themes 1, 3 and 4). These studies support a general inference that thematic distinctions within hexastylates are based on stereotyped structural differences.

Geochronologic History. Two lines of evidence have been used to infer the geochronologic history of the Hexastylate Mouthpart Class: the empirical fossil record (Fig. 115) and patterns of food resource use feeding mechanisms among primitive and derived cades of extant hexastylates. From this perspective the fossil record is more instructive

FIGURE 115. Geochronologic history of the Hexastylate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after McAlpine and Martin (1966), Rohdendorf (1980), Matile (1981), Hennig (1981), and Waters (1989a, 1989b) (but also see Wood and Borkent [1989] and Woodley [1989] for a differing view). The taxonomic level of analysis is the family. The outgroup is Tipuloidea. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.


MYA (x10^6)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
HEXASTYLATE MOUTHPARTS
TIPULOIDEA
Blepharoceridae
Deuterophlebiidae
Tanyderidae
Ptychopteridae
Eoptychopteridae
Nymphomyiidae
Psychodidae
Thaumeleidae
Simuliidae
Ceratopogonidae
Chironomidae
Chaoboridae
Culicidae
Dixidae
BIBIONOIDEA
Pelecorhynchidae
Xylophagidae
Stratiomyiidae
Acroceridae
Nemestriniidae
Pantophthalmidae
Tabanidae
Athericidae
Rhagionidae
ASILOIDEA
EMPIDOIDEA
See Fig.82
See Fig.109

since there are continuous records for many hexastylate families during the Mesozoic and Cenozoic. This relatively robust fossil record is attributable to three factors. They are (i) the presence of aquatic larval forms of most hexastylates that are preferentially deposited in those freshwater environments that are more likely to enter the sedimentological record than terrestrial environments, (ii) the exhaustive work of Soviet paleoentomologists in documenting insect-bearing stratal sections from lacustrine basins in Central Asia and (iii) the attraction of many adult nematocerans and brachycerans to exposed carbohydrate sources, including plant sap (Downes 1958, 1971) and their subsequent entrapment in Cretaceous and Tertiary ambers. Although hexastylates are well represented in the fossil record, there are some taxonomic families that are relatively enriched and others that are depauperate. Chironomids and rhagionids have the most continuous and frequently occurring records while psychodids, chaoborids, simuliids and ceratopogonids have sparse but still relatively continuous records. Although thaumeleaids, blepharocerids and dixids are represented in the Cretaceous, they have very poor fossil records, with one, two and three fossil occurrences respectively. Culicids and tabanids by contrast are more abundant but are confined only to the Cenozoic.

The earliest known hexastylate fossil occurrences are the architendipids *Architendipes tschnernovskii* Rohdendorf and *Palaeotendipes alexii* Rohdendorf from the Upper Triassic of the USSR [73] (Rohdendorf 1974). Although a diverse assemblage of plesiomorphic dipterans has been described by Rohdendorf (1974) as his suborder Archidiptera, nothing is known of their mouthpart structure. In a subsequent examination of upper Lower Jurassic to lower Upper Jurrasic insect faunas of Asia, Kalugina and Kovalev (1985) described modern-aspect hexastylate taxa from 21 localities of the Chulimo-Eniseykaya Depression [65], Upper Kusnetsk Basin, Irkutsk Basin [67] and the Zabaykakala Region [62,66]. These faunas yielded well-preserved larvae, pupae and adults of psychodids, chaoborids, chironomids and rhagionids that apparently bear well-preserved details of adult head structure. Kalugina and Kovalev's (1985) drawings and descriptions of these taxa are generalized and they unfortunately did not present higher magnifications for elucidation of informative head and mouthpart structures. Nevertheless these Jurassic forms exhibit the facies of the modern families to which they are assigned and undoubtedly were hexastylates. In somewhat younger Late Jurassic deposits [59,60] the earliest ceratopogonids and simuliids are documented (Grogan and Szadziewski 1988, Rasnitsyn 1988). In a study of a Lower Cretaceous lacustrine deposit from southern Australia [53], Jell and Duncan (1986) described simuliids, chironomids, chaoborids, dixids and rhagionids, most of which were similar to or assignable to extant subfamilies, tribes or genera. From Late Cretaceous and Tertiary ambers [45,37,36,35,19,17] numerous taxa often referrable to modern genera have been described (Boesel 1937; Hennig 1966, 1967; Remm 1976; Schlüter 1978; Larsson 1978; Keilbach 1982; Grogan and Szadziewski 1988).

Stylate, piercing-and-sucking mouthparts is probably plesiomorphous within nontipuloid nematoceran dipterans (Downes 1971) and this feeding style may have originated during the Triassic (Rohdendorf 1974) or may extend to the Permian (Tillyard 1935, Beklimishev 1957, Downes 1971). By the Early Jurassic, psychodid, culicoid and tabanoid styles of blood-feeding were present (Downes 1971). Prior to this time dipteran sanguinivory probably originated from a predatory habit wherein there was a subsequent shift from liquified insect tissues to vertebrate blood (see above section on "Diversity and Natural History" for exposition of a contrary view). Grogan and Szadziewski (1988) have indicated that blood-sucking is plesiomorphous for the Chironomidae and their sister-group, the Ceratopogonidae, and for the Chaoboridae and their sister-group, the Culicidae. These authors have also determined that insect predation and the habit of female ceratopogonid cannibalism of the male during copulation is derived.

This shift toward sanguinivory probably occurred relatively early in dipteran phylogeny since the primitive condition of four constituent culicoid families (Chironomidae + Ceratopogonidae, Culicidae + Chaoboridae) is sanguinivory and one family from each pair has a fossil record extending to the Early Jurassic [66] (Fig. 115). Although currently these culicoid families are primitively and dominately sanguinivorous on modern aspect warm-blooded mammals, their occurrence in various Cretaceous and Jurassic deposits (Remm 1976, Kalugina and Kovalev 1985, Grogan and Szadziewski 1988) raises the question of the identitiy of their Mesozoic hosts. Endothermic mammals, birds and derived dinosaurs are known from the Cretaceous and ancestral primitive mammals have a fossil record dating to the Early Jurassic (Kemp 1985). Presumptive warm-blooded therapsids are well-documented from the Triassic (Carroll

1988). However recent documentation of sanguinivory on cold-blooded vertebrates by taxa representing most hexastylate familes (*vide supra*) indicates that tetrapods such as lissamphibians, turtles, lizards and archaic ectothermic dinosaurs also could have been hosts for early sanguinivorous hexastylates.

Previous Designations. The distinctiveness of the mosquito mouthpart type for feeding was recognized by Aristotle during the Third Century B.C. In his *De Partibus Animalium*, Aristotle categorized those insects that lacked teeth (i.e. mandibles) and possessed a proboscis into three classes, one of which was those forms "sucking blood only," for which mosquitoes were cited as an example (Morge 1973). Approximately two millenia later Fabricius (1775) included the Antliata in a group with sucking mouthparts. The Antliata was defined as dipterans with seta-bearing proboscides. (In this context the term, seta, refers to a stylet). Subsequently, during the latter half of the 1800's and the early 1900's, there were numerous articles illustrating and describing the stylate mouthparts of adult nematocerans, including those by Dimmock (1881), Smith (1890, 1898), Packard (1898), Kellogg (1899), Wesché (1902, 1904, 1909), Dell (1903), Emery (1913), Cragg (1913a) and Peterson (1916). By the late 1920's enough was known about the mouthparts of adult stylate dipterans that Metcalf (1929) considered a "common biting fly or dipterous subtype," which was subdivided into several kinds, one of which was the "first subtype: the mosquito," recognizing that the "second subtype: the horse fly" was qualitatively different (Table 6). During this time and later there was growing appreciation of the structural differences among various nematoceran and brachyceran mouthpart types, with Matsuda (1965), Denis and Bitsch (1973), Smith (1985) and Chaudonneret (1989b) all devoting separate sections in their mouthpart reviews for discussions of several, family-based, mouthpart types (*vide supra*).

For most adult nematoceran and brachyceran taxa comprising the hexastylate mouthpart class, several terms have been used to refer to characteristic themes within the class. Gillett (1971) used the term "fasicle" to refer to the mouthpart ensemble of mosquitoes. Jobling (1976) coined the term "syntrophium" to designate the united stylets of black flies and McAlpine (1981) appropriated the term "proboscis" to refer to all dipteran mouthparts. The first two terms are nomenclaturally confined to particular taxonomic families; the last term is a general designation that historically has included any prolongation of mouthparts of hexapods. I am using the new term **hexastylate** to refer to the characteristic mouthparts discussed in this section. It has not been used previously in the literature.

Review of Literature. Hexastylates are the most well-documented of all mouthpart classes, averaging approximately five references per taxon (Appendix B). This profusion of documentation is attributable to the medical and economic importance of many hexastylates as vectors of pathogen-borne diseases. Work in the study of adult nematoceran and brachyceran piercing mouthparts began early in the 1900's and was expanded during the 1920's to 1950's after the life- cycles and intermediate hosts of several nematoceran-vectored pathogens were known. This was particularly true in tropical and subtropical areas where human-inflicting diseases such as elephantiasis, yellow fever, malaria and dengue fever (all vectored by Culicidae), onchoceriasis (Simuliidae vectors), leshmaniasis, kala-azar and verrunga (Psychodidae vectors) and tularemia and animal trypansomiasis (Tabanidae vectors) were brought under various levels of control by insect abatement and eradication programs.

Major sources for head and mouthpart data are principally studies of the mouthpart structure of a single, or infrequently a few, dipterans that usually are of medical or economic importance. For the Psychodidae, Adler and Theodor (1926) described *Phlebotomus papatasii* Scopoli, Shortt and Swaminth (1928) worked out the transmission of kala-azar flagellates of *Phlebotomus argentipes*, and Lewis (1975) studied the functional morphology of phlebotomine mouthparts. For the Culicidae, Dimmock (1881) presented one of the earliest investigations of *Culex* sp. mouthparts, Robinson (1939) described in detail female *Anopheles meigeni* mouthparts and Schiemenz (1957) provided an excellent examination of the head and mouthparts of *Culiseta annulata* (Schrank). Shorter studies of culicids include Kulagin (1905) for a study of the cranial structure of *Culex* and *Anopheles*, Vogel (1921) for the microstructure of the piercing apparatus of culicids and tabanids, Sinton and Covell (1927) who examined the relationship between buccal cavity structure and anopheline classification, Barraud and Covell (1928) for determining buccal cavity form, and Wenk (1961) for an investigation of culicid mandible musculature. Among the Simuliidae, Emery (1913) described *Simulium vittatum* Zetterstedt and Gibbins (1938) examined *Simulium damnosum* Theobald.

Shorter contributions to knowledge about simuliids were Nitzulescu's (1926b) study of the structure of *Simulium* mouthpart structure by use of microscopic cross-sections, Krafchick's (1942) study of the mouthparts of *Eusimilium lascivum* Twinn, and Nicholson's (1945) comparison of mouthparts of *Cnephia dacotense* (Dorogostuski) and *Simulium venustum* Say. Ceratopogonids have been examined by Gad (1951), who described head and mouthpart structures of *Culicoides impunctatus* Goetzee, *Atrichopogon pavidus* Winnertz and *Dichrobezzia venusta* Meigen and provided valuable data on diets, by Wenk (1962) for *Wilhelmia equina* Linneaus, and by Sutcliffe and Deepan (1988) who documented the structure and function of mouthparts of *Culicoides sanguisaga* (Coquillet) by use of scanning electron microscopy. Tabanids have been extensively documented by the research of Cragg (1912a) for mouthpart structure in *Haematopota pluvialis* (Meigen); Mitter (1918), Tetley (1918) and Nitzulescu (1927a) for stimulating but somewhat contradictory interpretations of the extremely long and much-noted proboscis of *Corizoneura longirostris* Hardwick; Bonhag (1951) for a study of mouthparts from *Tabanus sulcifrons* Marquardt; and Stoffolano and Yin (1983) for examination of *T. nigrovittatus* Marquardt. Shorter contributions include Lall and Davies (1971) for a comparison of cephalic structures of three tabanid species and Suvarova (1985) for various tabanid mouthpart structures.

Numerous comprehensive studies and reviews of hexastylate mouthparts are available. Early syntheses of nematoceran and brachyceran structure can be found in Kellogg (1899), the detailed monograph of Peterson (1916), Crampton's (1942) extensive study of fly anatomy, and

Ferris (1942) and Hoyt (1952) who examined dipteran head structure in the context of phylogeny. Shorter accounts focusing on selected mouthpart structures from a few representative families are Wesché (1902, 1904, 1909), Cragg (1913a), Lindner (1919) and Grenier (1959). Snodgrass (1943, 1944, 1959) produced a series of accounts on the head and mouthpart structure of piercing-and-sucking dipteran families. More recently general summaries of mouthpart structure have been provided by Matsuda (1965), Denis and Bitsch (1973) McAlpine et al. (1981, 1987), Smith (1985) and Chaudonneret (1989b).

Recent morphological studies that use transmission- and scanning-electron microscopy (SEM) techniques have increased greatly information on nematoceran and brachyceran mouthparts and stylet structure. McKeever (1986) examined the stylet structure of four species of the chaoborid *Corethella*; Hudson (1970) figured the stylet microstructure of the culicids *Aedes stimulans* Walker, *A. atropalpus* Coquillet, and *Wyeomyia smithi* Coquillet. Sutcliffe and McIver (1984) and Sutcliffe (1985) described the mouthpart anatomy of the simuliid *Simulium venustum* Say, and McKeever et al. (1988) examined the mouthparts of four species of the ceratopogonid *Culicoides*. Additional SEM studies include Zaitzev (1982) for an exploration into denticle type and pseudotracheal ornamentation of culicids, rhagionids and tabanids, and Stoffolano and Yin (1983) for a description of the mouthparts of the tabanid *T. nigrovittatus* Marquardt.

8.9.8. Tristylate Class
(Class 30)

Description. Head quadrate; proboscis long to very long; genal combs often present. Genae expanded dorsoventrally over the cranium; gula moderately to minimally developed. Antennae spathulate; ocelli 2; compound eyes absent. Mouthparts hypognathous, protractile, stylate-haustellate, consisting of 3 stylets. Food pump clypeal and pharyngeal.

Clypeus indistinguishably fused to frons. Labrum a quadrate or ventrally-elongate nasale, margin a beak brace. Hypopharynx a salivary syringe with a piston pump; epipharynx stylate and adjoined to labrum. Mandibles absent. Maxilla with basal stipital fusion to adjacent sclerites; bearing a palpus, galea and lacinia. Palpus 4-segmented, filiform-clavate, long to very long. Galea a robust lobe used as a lever for lacinial stylet protraction; lacinia stylate, acuminate and long. Labium with 2 basal segments; glossae and paraglossae absent. Labial palpi housing stylets when appressed; generally 4-segmented, uncommonly otherwise; length variable. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. Several unique features characterize the tristylate mouthpart class. The unique lacinial stylet protaction mechanism occurs only among tristylates. This mechanism involves a robust, elongate galeal lobe that is used as a lever which is pushed posteriorly for forward and downward engagement of the attached lacinial stylet. Another unique condition is the combination of a single epipharyngeal stylet and two lacinial stylets. The presence of spathulate antennae is found only in tristylates although the scrobinate cavities in which they rest is also found in rhynchophorates (Section 8.3.10). A final characteristic feature of tristylates is modified labial palps with excavate mesial surfaces that envelop the three stylets during palpal appression. These palps act as separate, unjoined units during times other than feeding.

Tristylates are contrasted with various stylate-haustellate mouthpart classes with a dipteran facies, namely the monostylate/distylate, distylate/tetrastylate and hexastylate mouthpart classes (Sections 8.9.5 to 8.9.7). However these three mouthpart classes have head-related features typical of free-living, predaceous species and includes large compound eyes, aristate or plumose antennae and a prominent, labial haustellum ensheathing mouthparts at all times. An additional difference is the absence of dipteran taxa with three stylets in the three above mouthpart classes. Mouthcones (Section 8.9.3) bear three stylate mouthpart elements, but have head and mouthpart asymmetries that are not found in tristylates.

Diversity and Natural History. The tristylate mouthpart class consists of small, wingless, laterally-compressed ectoparasites that are highly specialized, obligate sanguinivores on birds and mammals (Fig. 116). Tristylates, also known as fleas, are an important component of an assemblage of five stylate-haustellate mouthpart classes that are either obligate sanguinivores or are dominated by sanguinivorous species. This suite comprises the buccal-cone, hexastylate, tristylate, tubulostylate and siphonostylate mouthpart classes (Sections 8.9.3, 8.9.7 to 8.9.10). The taxonomic diversity of tristylates is modest,

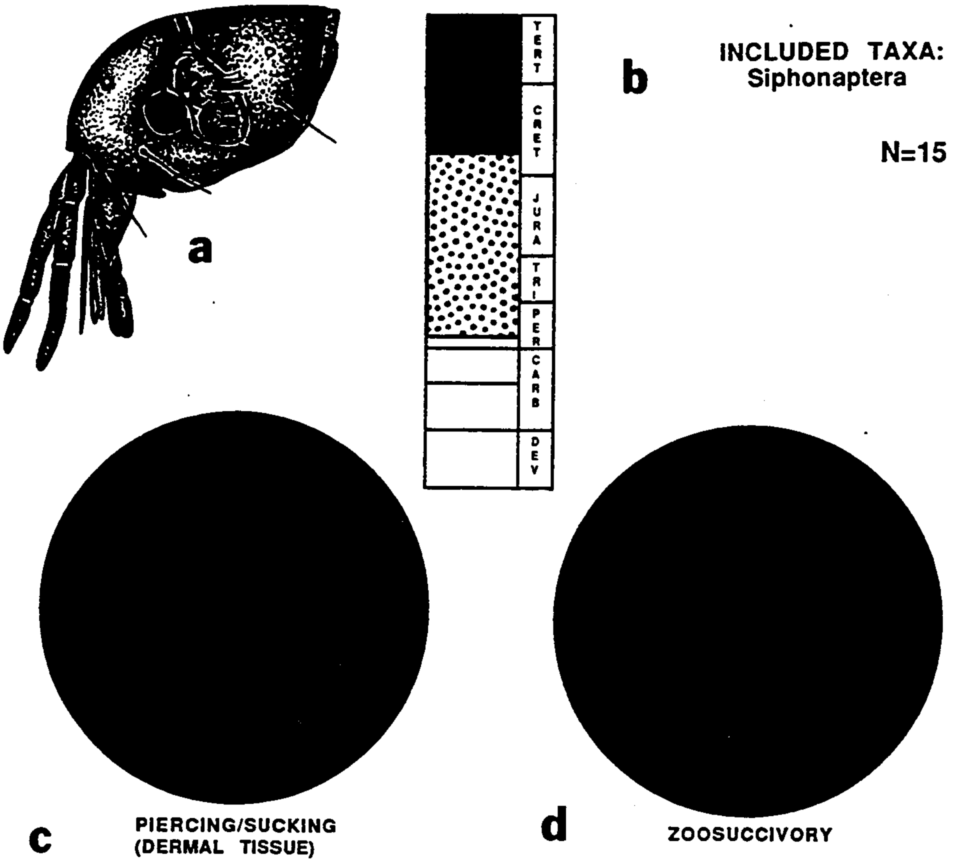


FIGURE 116. Overview of the Tristylate Mouthpart Class. a, *Pulex irritans* Linneaus, female (Siphonaptera, Pulicidae, data-set no. 789); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-group; d, dietary spectrum.

comprising 15 families, 222 genera and 1700 species (Appendix D) and it contributes a minor proportion to the modern insect fauna, ranking 25 out of 34 mouthpart classes (Table 5, Fig. 131). Tristylates are inconspicuous, rarely encountered elements of modern terrestrial ecosystems. Strong evidence indicates that the tristylate mouthpart class is monophyletic (Kristensen 1981). However, if the bizarre, Late Cretaceous saurophthirid is included (*vide infra*, not analyzed in this study), its possible independent derivation from a mecopterous stock may indicate convergence within the class.

Tristylates feed by aspirating blood into the pharynx after mixing the imbibed fluid with a salivary gland-secreted anticoagulant that is injected at the puncture site (Brues 1972). Feeding can continue up to four hours in some species, during which blood passes through the alimentary tract in a minimally processed state (Marshall 1987). In most instances feeding intervals are shorter and nutritional uptake from blood is significantly more efficient. The resistance to food deprivation is well-established in tristylates: *Nosopsyllus fasciatus* (Bosc) remains up to 450 days as a pupa without food and adults have been documented as viable up to 120 days after pupation without a blood meal (Marshall 1987). In fact, adult fleas live longer if subjected to temporary starvation after pupation than if immediately fed (Suter 1964). Although adults can remain alive for considerable periods with food, females require a blood meal before ovipositing fertile eggs (Richards and Davies 1977).

Tristylates are highly stereotyped structurally (Price 1980) and possess several adaptations for clinging to and moving on the hosts, such as genal combs (Traub 1980a) and clasping tarsi. Host recognition by negatively phototactic tristylates is accomplished by actively responding to warmth, body odor and body movements of a potential host (Marshall 1987). Although tristylates require an endothermic vertebrate host (bird, mammal) and many species have high specificities for certain host species (Brues 1972), they nevertheless can live on related or even nonrelated species for extended durations, and often will readily transfer if a suitable host is available (Richards and Davies 1977). Recent evidence indicates however that tristylates are much more host-specific for reproductive purposes than for feeding purposes. As a group, tristylates exhibit a much broader spectrum of life-cycle patterns than other ectoparasites, ranging from vermipsyllids that are periodically free-living in pastures of the adult hosts to the obligately host-specific *Tunga monositius* Linneaus, in which adult males are nontrophic and females must burrow subdermally in the host to remain viable (Marshall 1987). Although tristylates are generally found on host bodies, many spend part of their life-cycle residing in the nest of their host, where they may infect other adult or newly-born individuals of the same host species.

Structural Themes. The dendrogram of the Tristylate Mouthpart Class (Fig. 117) may exhibit two structural themes. Characters contributing to the differentiation of tristylates into these two themes include differences in proboscidal length, presence or absence of a genal comb, labral shape and probably the aspect-ratio of the maxillary palpus. However these features are not major and substantiate the

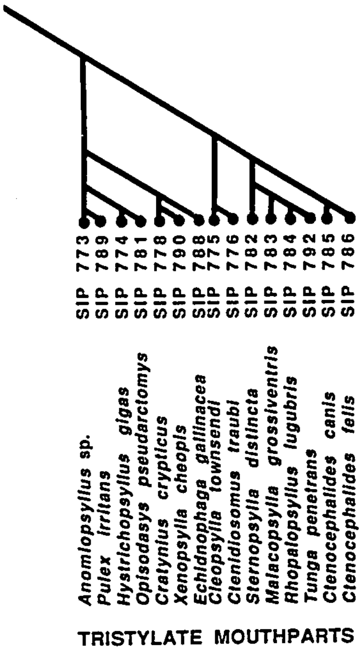

SIP 773 Anomiopsyllus sp.
SIP 789 Pulex irritans
SIP 774 Hystrichopsyllus gigas
SIP 781 Opisodasys pseudarctomys
SIP 778 Cratynius crypticus
SIP 790 Xenopsylla cheopis
SIP 788 Echidnophaga gallinacea
SIP 775 Cleopsylla townsendi
SIP 776 Ctenidiosomus traubi
SIP 782 Sternopsylla distincta
SIP 783 Malacopsylla grossiventris
SIP 784 Rhopalopsyllus lugubris
SIP 792 Tunga penetrans
SIP 785 Ctenocephalides canis
SIP 786 Ctenocephalides felis
TRISTYLATE MOUTHPARTS

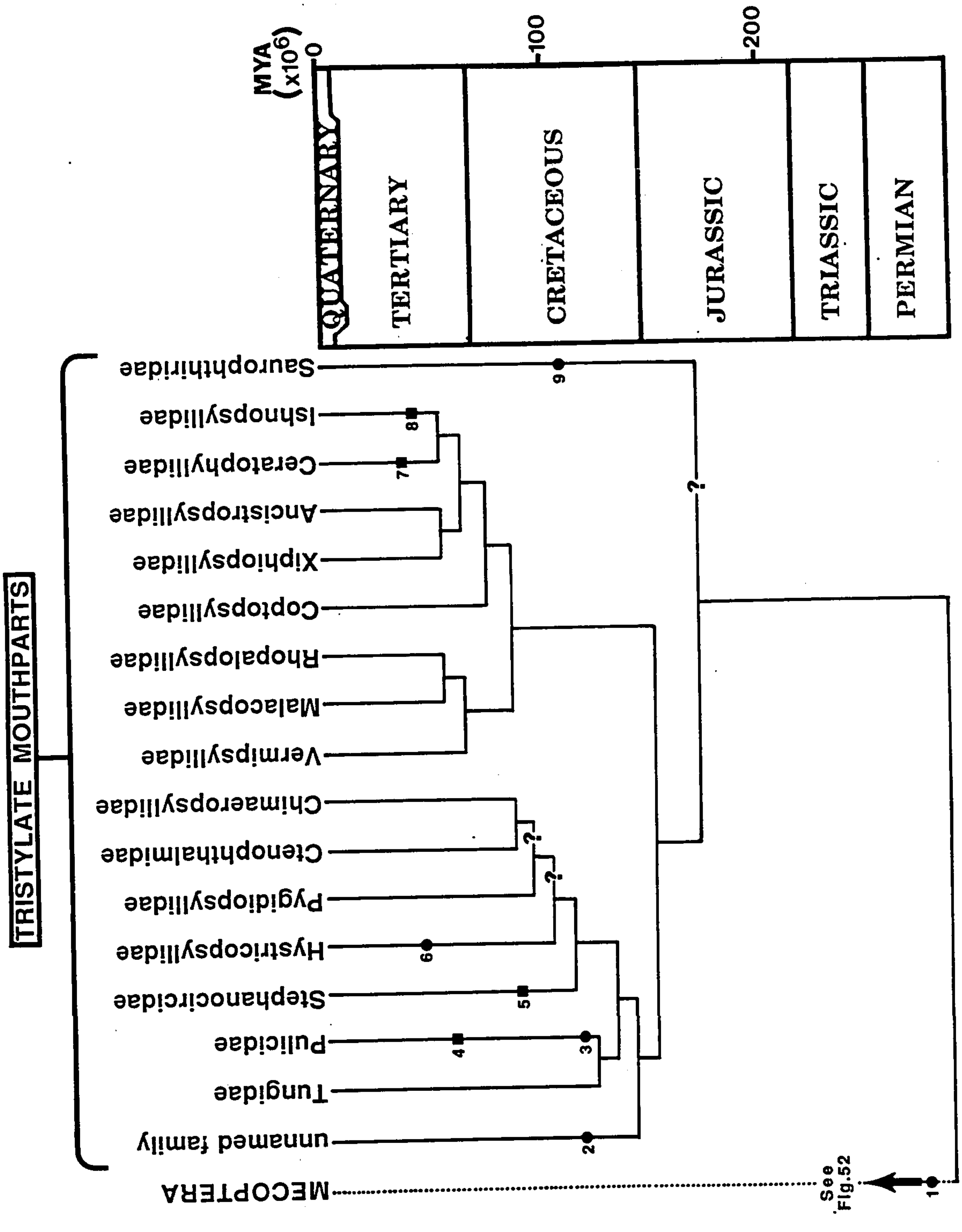
FIGURE 117. Cluster analysis dendrogram of taxa comprising the Tristylate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

claims of some (Richards and Davies 1977, Price 1980) that siphonapterans are a very structurally uniform group.

Geochronologic History. The earliest known fossils of the Tristylate Mouthpart Class are four siphonapteran species recovered from Lower Cretaceous deposits of southern Australia [53] (Riek 1970, Jell and Duncan 1986) (Fig. 118). Although the siphonapteran affinity of these four species have been questioned by some (Willmann, *in* Hennig 1981), they exhibit several synapomorphies that define modern siphonapterans, including a laterally compressed body, pronotal combs, lacinial stylets and siphonapteran-type genitalia. From this deposit Jell and Duncan (1986) described two unnamed pulicids, one of which was considered ancestral to the modern pulicid *Echidnophaga* (Riek 1970), and two named species that have not been assigned to a family. One of these, *Tarwinia australis* Jell and Duncan 1986, is excellently preserved.

In slightly younger deposits of the USSR [52], Ponomarenko (1976) described an enigmatic insect that possesses some mecopteran features, but was assigned to the Siphonaptera by the author. This fossil, *Saurophthirus longipes* Ponomarenko 1976, has a relatively large (1.2cm long) body, long legs, abbreviated clavate antennae and opistognathous, stylate-haustellate mouthparts similar to *T. australis* from Australia. Unlike the Australian forms, *S. longipes* is dorsoventrally compressed, has a large genal expansion of the cephalic sidewall and a vestiture of dense, small spinules. The proposed host of *S. longipes* is a pterosaur, based on the possession of structures that are similar to those found on

FIGURE 118. Geochronologic history of the Tristylate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylogram is after Beier (1938), Traub and Rothschild (1983) and Kristensen (1981). The level of taxonomic analysis is the family. The outgroup is Mecoptera.


MYA (x10^6)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
TRISTYLATE MOUTHPARTS
Saurophthiridae
Ishnopsyllidae
Ceratophyllidae
Ancistropsyllidae
Xiphiopsyllidae
Coptopsyllidae
Rhopalopsyllidae
Malacopsyllidae
Vermipsyllidae
Chimaeropsyllidae
Ctenophthalmidae
Pygiodopsyllidae
Hystricopsyllidae
Stephanocircidae
Pulicidae
Tungidae
unnamed family
MECOPTERA
See Fig.52
1
2
3
4
5
6
7
8
9
?
?
?

extant parasites of bats (Ponomarenko 1976). Ponomarenko (1976) referred *S. longipes* to the Siphonaptera, whereas Dmitriev and Zherikin (1988) and Rasnitsyn (1988) assigned the same fossil to the Mecoptera, and Waage (1979) hinted that it may be an ordinally distinct lineage. In significantly younger Baltic amber deposits [19], two hystricopsyllid siphonapterans, *Palaeopsylla klebsiana* Dampf 1910 and *P. dissimilis* Peus 1968 have been described and are recognized as modern genera (Larsson 1978).

Complementing this spotty fossil record (Fig. 118) is better-documented but indirect data on the zoogeographic and phylogenetic relationships of siphonapteran host mammals. From an exhaustive analysis of geographic distributions in time and space and of the phylogenetic relationships of host clades, (Traub 1980b) and Traub and Rothschild (1983) have inferred major events during the history of the tristylates. (Much of the ensuing discussions originates from these two sources.) For tristylates primitive hosts bear primitive parasites and derived hosts bear derived parasites, with some exceptions. When there has been a geochronologically recent lateral transfer it has not involved mammalian hosts "lower" on the taxonomic scale. It appears that the more primitive families of siphonapterans have austral relationships associated with a late Gondwanan distribution and emphasized parasitism on various marsupial groups. These siphonapteran families antedate modern mammalian families and may precede the appearance of extant eutherian orders, although some family-level differentiation has occurred after the fragmentation of Gondwanaland.

The ultimate origin of siphonapterans probably stems from a boreid-like mecopteran (Tillyard 1935, Schlein 1980) during the Late Paleozoic or Early Mesozoic. Marsupials arose in South America during the Late Jurassic to Early Cretaceous (Lillegraven 1974) and they dispersed to Australia via Anarctica by the later Early Cretaceous, carrying with them stephanocircid and doratopsylline siphanopterans (Traub 1980b). Thus evidence indicates that siphonapterans were probably in existence by the Late Jurassic and certainly occurred during the Early Cretaceous, based on paleobiogeographic evidence. Fossil evidence indicates that Early Cretaceous siphonaperans with combinations of apomorphic and plesiomorphic characters occurred in Australia (Jell and Duncan 1986). Although South America was also the center of origin of rhopalopsyllids and malacopsyllids, where they currently only occur, they are not found in the Australian fauna and probably evolved after the Early Cretaceous. Subsequent marsupial migrations back to South America from Australia resulted in establishment of pygidiopsyllids (e.g. *Ctenidosomus*) in South America. By Baltic amber times [19] the presence of the advanced, rodent-inhabiting *Palaeopsylla*, a modern hystricopsyllid genus, led Larsson (1978) to posit a Mesozoic origin for the family because of the presence of hystricopsyllids on Australian marsupials. At about the same time, ctenophthalmine pulicids that originated in Africa colonized South America and later North America presumably by rafting of hystricomorph rodents and ceboid monkeys across the Atlantic Ocean. In summary, while data for an Early to Middle Mesozoic presence for tristylates is absent, two independent lines of evidence indicates their presence and family-level diversification during the Late Mesozoic.

Previous Designations. Probably because of their small size, the mouthpart condition of siphonapterans did not significantly enter the entomological literature until the early 1800's. During this time MacLeay (1821) classified insects by mouthpart type (Mandibulata versus Haustellata) and type of larval and pupal stage present, applying the term "Aptera" for those insects with haustellate mouthparts, active larvae and a dormant, free pupa. Kirby and Spence (1826) used the new designation "Aphaniptera" for the Suctoria of Leach and Latreille and recognized their possession of suctorial mouthparts. Latreille (1832) later renamed his Suctoria as Siphonaptera. During the past century Metcalf (1929) categorized siphonapteran mouthparts as a "flea or siphonapterous subtype" of the piercing-sucking type within the Haustellate Series (Table 6). The same designation was used by Metcalf et al. (1962), although shortly thereafter James and Harwood (1969) considered the distinctive mouthparts of siphonapterans simply as "the siphonapteran type." Recently, Chaudonneret (1989a) has recognized the structural uniqueness of siphonapteran mouthparts, considering them a subordinate theme within piercing-type mouthparts.

In the above discussion, the confounding of taxonomic and functional (or process-centered) terms as names for a mouthpart type leaves little room for explicit reference to a particular, distinctive structure. Because members of this mouthpart class uniquely possess three haustellar stylets as mouthpart elements, I am using the structurally informative term **tristylate** as a name for this mouthpart class.

Review of Literature. Data sources for tristylate head and mouthpart morphology are limited and are characterized by a lack of mouthpart descriptions from Southern Hemisphere taxa, particularly Africa and Australia. Only a few morphological and functional-morphological works are available, including Lass (1905) for *Pulex canis* Dugés, Rothschild (1906) for *Xenopsylla cheopis* Rothschild, Snodgrass (1946) for a comprehensive monograph on the structue of many siphonapteran species and Wenk (1953) for *Ctenocephalus canis* (Curtis). Shorter works on mouthpart structure include Nitzulescu (1927) for epipharyngeal stylet structure, Heymons (1937) for the role of mouthpart structure in the systematic position of the Siphonaptera and Wenk (1980) for the mechanism of stylet penetration. Hopkins and Traub (1955) have discussed the head and mouthpart structure of *Cratynius crypticus* Hopkins and Traub. Johnson (1957) classified all known siphonapterans from South America, describing and illustrating eight families, many of which are poorly known and confined only to that continent. Extended brief reviews of tristylate mouthparts can be found in Matsuda (1965), Denis and Bitsch (1973), Smith (1985) and Chaudonneret (1989a).

8.9.9. Tubulostylate Class
(Class 31)

Description. Head quadrate; proboscis short to long; prothorax enveloping dorsal head region. Genae and gula generally well-developed. Antennae pectinate/plumose or aristate; ocelli absent, rarely 3; compound eyes variously developed. Mouthparts prognathous, stylate-haustellate, monostylate, protractile. Food pump clypeal and pharyngeal.

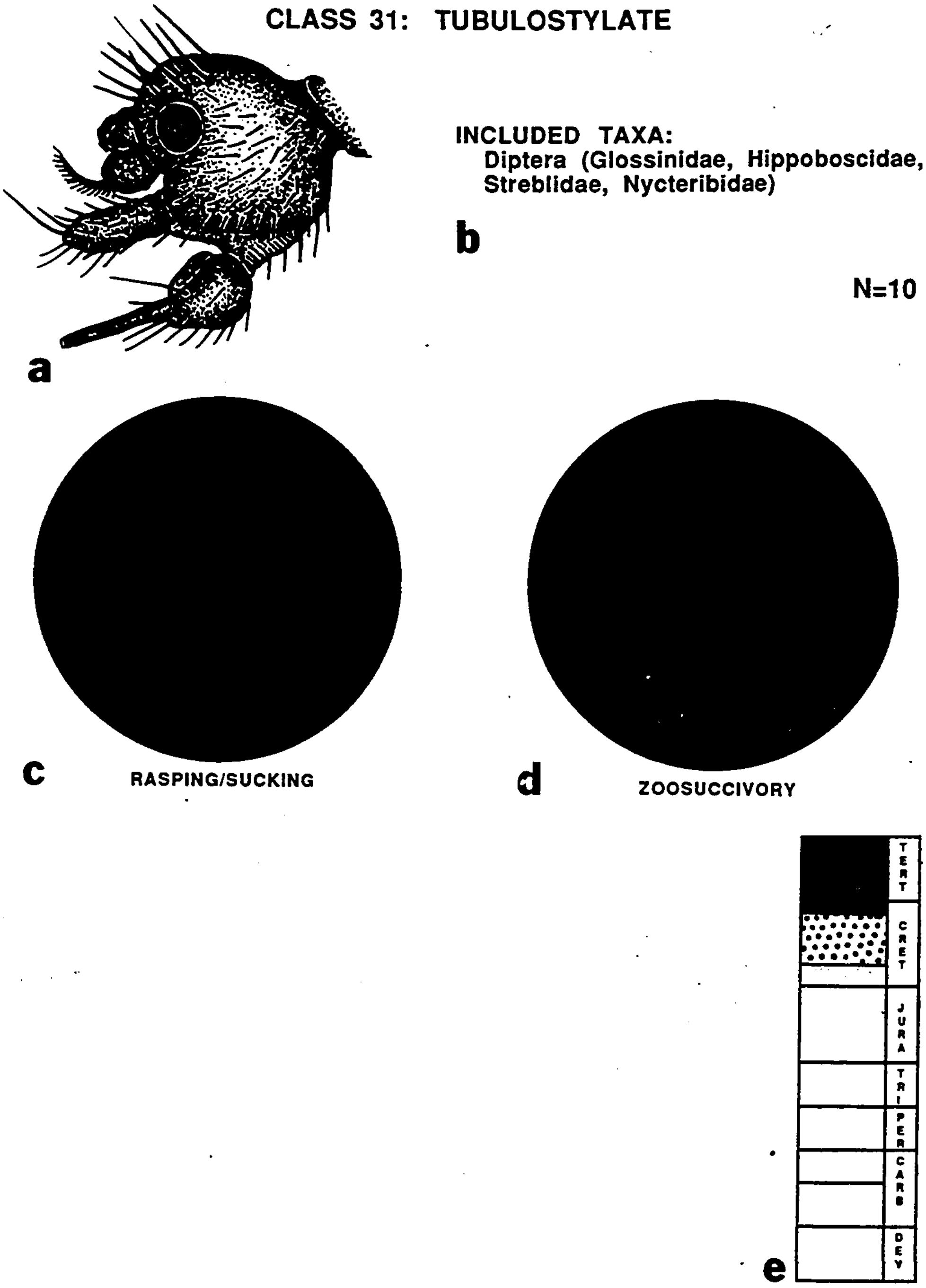
Clypeus quadrate, infrequently transversely-elongate; fused to frons. Labrum vertically very elongate, undivided or divided, margin mucronate/acuminate. Hypopharynx a bulbous reservoir terminating in an apertuate lobe; epipharynx fused to labrum. Mandibles absent. Maxilla with one basal, rodlike sclerite (stipes); bearing a palpus only. Palpus 1-segmented, pectinate, short to intermediate in length, rarely otherwise. Galea and lacinia absent. Labium with one basal sclerite; bearing palps. Palpi tubular, 3-segmented, length variable. Glossae and paraglossae absent. Interregional co-optation of mouthpart elements present.

Key Phenocharacters. Two combinations of characters uniquely define the tubulostylate class. The stylet in tubulostylates is a long, tubular labellum with sharp, terminal denticles. Additionally, the combination of absence of mandibles, galeae, laciniae, glossae and paraglossae, and the presence of a well-developed proboscis with "pharyngeal" and labial elements is diagnostic.

Tubulostylates resemble the siphonostylate mouthpart class (Section 8.9.10), although the functional mouthpart stylet is a labellum in the former and a galeal siphon in the latter. Although the similarities of a general dipteran facies exists between labellates (Section 8.5.3) and tubulostylates, labellates possess a fleshy, distally-expanded labellar sponging organ whereas tubulostylates have modified the same homolog into a tubular stylet with terminal, piercing denticles. Additional differences between the two mouthpart classes is the presence of three ocelli and a membranous rather than a haustellate-involved epipharynx in labellates.

Diversity and Natural History. The Tubulostylate Mouthpart Class is an obligately sanguinivorous (Fig. 119), ectoparasitic group of mostly small (0.10 to 1.2cm long), highly derived cyclorrhaphan flies with unique feeding, reproductive and life-cycle adaptations for living on avian and mammalian (often bat) hosts. Tubulostylates consist of the families Glossinidae, Hippoboscidae, Nycteribiidae and Streblidae. There apparently are no taxa connecting these four monophyletic families (McAlpine 1989) to nonsanguinivorous, free-living cyclorrhaphans with typical labella (Waage 1979). The tubulostylate class comprises four families, 57 genera and 712 species (Appendix D) and is the 27th most diverse mouthpart class in terms of species (Table 5, Fig. 131). Consequently tubulostylates are not important in the structuring of modern terrestrial communities.

With the exception of glossinids, members of this mouthpart class are adept at clinging to hosts and virtually all work their way through hair and feathers, reaching the skin surface where they imbibe blood by a specialized tubular proboscis. Both sexes feed on blood (Richards and Davies 1977), although there is sex-based mouthpart dimorphism in some forms. The larval stage is not free-living and is extruded vivaparously by the female, after which it immediately undergoes tanning and pupation (Waage 1979). Hippoboscids are ectoparasites on birds and to a lesser



INCLUDED TAXA:
Diptera (Glossinidae, Hippoboscidae, Streblidae, Nycteribidae)

FIGURE 119. Overview of the Tubulostylate Mouthpart Class. a, *Trichobius caecus* Edwards (Diptera: Streblidae, data-set no. 1019), after Jobling (1929); b, taxonomic distribution and number of taxa examined; c, functional-feeding-group; d, dietary spectrum; e, geochronologic range.

degree on ungulate mammals; nycteribiids and streblids are obligate parasites on bats; and glossinids are unattached sanguinivores on reptiles and ungulate mammals but will attack humans (Buxton 1955, Maa and Peterson 1987, Peterson and Wenzel 1987, Wenzel and Peterson 1987). The only known example of endoparasitism these groups is the unusual female of the streblid *Ascodipteron*. *Ascodipteron* crawls to the skin surface, casts off her wings and legs, and then burries herself subcutaneously, where she is transformed into a blood-engorging, sacciform endoparasite (Wenzel and Peterson 1987).

Many tubulostylates are host-specific; some are restricted to two or three congeneric host species; and a few lack host preferences, with hosts ranging from relaed or unrelated genera in the same family or different families of hosts (Buxton 1955, Maa and Peterson 1987, Peterson and Wenzel 1987, Wenzel and Peterson 1987). For nycterbiids some species parasitize several species in different genera or families; conversely there are bat species that harbor multiple nycterbiid and other ectoparasites (Richards and Davies 1977). Also, the geographic distribution of hosts is not congruent with respective parasite distribution, since competition from other ectoparasites and morphological variability of host populations (e.g. host hirsuteness and hair distribution patterns) may restrict the parasite to a portion of the host range (Peterson and Wenzel 1987). Thus nonspecific host associations, especially for glossinids and hippoboscids, are determined more by ecological and physiologic factors than by the phylogenetic relationships of the hosts (Buxton 1955, Maa and Peterson 1987). Several senses are used in host-seeking behavior, including visual detection by glossinids and hippoboscids of ungulate hosts and olfactory recognition of bat hosts from their urine and carbon dioxide by streblids and nycteribiids (Buxton 1955, Marshall 1987).

All tubulostylates are obligate sanguinivores (Fig. 119). After pupal emergence tubulostylates usually feed within minutes to a few hours on their host. Some species such as *Melophagus ovinus* Linneaus feed approximately every 36 hours (Nelson 1955) whereas glossinids feed approximately once a day, though they can survive missing a daily meal (Buxton 1955). (Glossinids are the vector for the transmission of trypanosomes to mammals, including various trypanosomes that cause African sleeping sickness in humans.) Similar feeding frequencies have been reported for hippoboscids with avian hosts (Popov 1955). Once starved, hippoboscids on mammalian hosts live only about a week (Popov 1965), although hippoboscids on avian hosts survive from one to three days without food (Marshall 1987). By contrast the streblid *Trichobius joblingi* feeds every few minutes and will survive only four hours without food; most streblids die within a day when starved (Wenzel and Peterson 1987). The rate of blood imbibation is frequently impressive: a female glossinid was recorded to imbibe 77.5mg of blood at a single feeding (Buxton 1955). Hippoboscids can imbibe during five to 30 minutes blood meals weighing from 40 to 160% of their own body weight (Nelson and Petrunia 1969). Recent studies have indicated that the ingested blood meal is deficient in certain nutrients, particularly B-complex vitamins, that may be supplied by gut symbiotic bacteria (Marshall 1987).

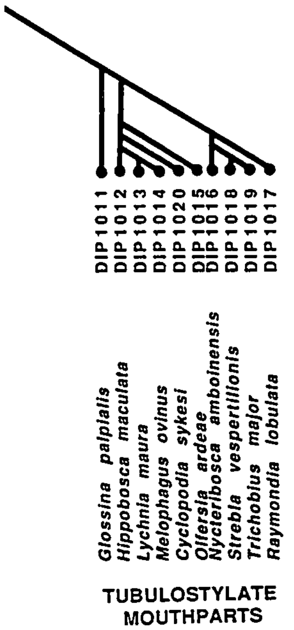

DIP1011 Glossina palpialis
DIP1012 Hippobosca maculata
DIP1013 Lychnia maura
DIP1014 Melophagus ovinus
DIP1020 Cyclopodia sykesi
DIP1015 Olfersia ardeae
DIP1016 Nycteribosca amboinensis
DIP1018 Strebla vespertilionis
DIP1019 Trichobius major
DIP1017 Raymondia lobulata
TUBULOSTYLATE MOUTHPARTS

FIGURE 120. Cluster analysis dendrogram of taxa comprising the Tubulostylate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

Structural Themes. Two discrete structural themes are recognized within the Tubulostylate Mouthpart Class (Fig. 120). The first theme consists of the single glossinid taxon, *Glossina palpialis* Robineau-Desvoidy (Subcluster 1, data-set taxon 1011 in Fig. 120) and the second theme comprises the remaining taxa of hippoboscids, nycteribiids and streblids (Subcluster 2, taxa 1012 to 1017). Features that distinguish the glossinid from the second subcluster include (i) moderate- to minimally-developed rather than prominent and well-developed genae and gula, (ii) three ocelli rather than ocellar absence, (iii) a spinose labrum rather than a labrum otherwise ornamented, (iv) a maxillary palpus that is very long and filiform rather than short- to intermediate in length and pectinate and (v) a labial palpus whose terminus is more fleshy than rigid. Although there is apparent subclustering within the second theme, only three characters consistently define the two apparent groups."

Geochronologic History. The fossil tubulostylate record is poor, with only three localities yielding material (Fig. 121). Two fossil occurrences are known for glossinids, *Eophlebomyia clavipennis* Cockerell 1925 from the Middle Eocene of Wyoming [23] and a more recent occurrence of four *Glossina* specimens from the Early Oligocene of Colorado [15]. A single hippoboscid, *Ornithomyia rottensis* Statz is known from the Late Miocene of Germany [2] (Maa 1966). Streblids and nycteribiids lack a fossil record (Peterson and Wenzel 1987, Wenzel and Peterson 1987), although their obligate bat hosts are traceable to the Middle Eocene [23] (Grande 1980).

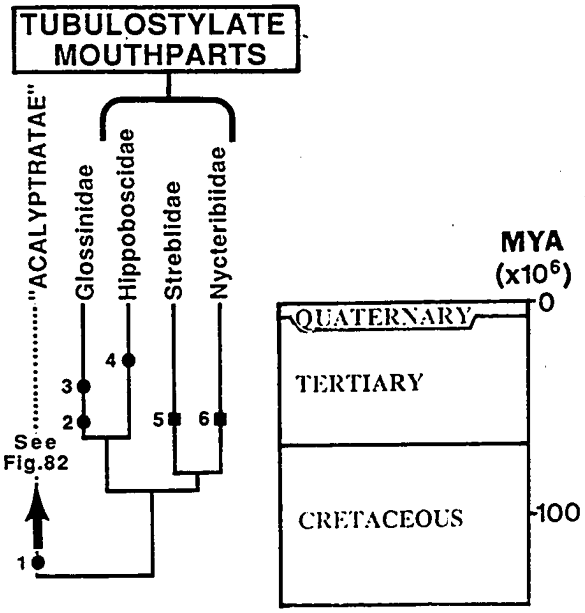


FIGURE 121. Geochronologic history of the Tubulostylate Mouthpart Class. See Appendix F for taxa, localities and referenes corresponding to each fossil occurrence. The phylogram is after McAlpine (1989). The level of analysis is the family. The outgroup is Acalyptratae

A recent analysis of the cladistic relationships among pupiparous and related dipteran families (McAlpine et al. 1989) indicates that the Acalyptratae is the sister-group to the ([Glossinidae + Hippoboscidae] + [Nycteribiidae + Streblidae]) clade. The earliest fossil occurrence of the Acalyptratae is a conopid from Early Cretaceous Lebanese amber [55] mentioned by Hennig (1971). This indicates that the stem-group of the four tubulostylate families occurred as early as the Early Cretaceous although the radiation of tubulostylates on various mammalian ruminant and bat hosts, and avian hosts probably occurred during the Early Tertiary, based on host and parasite fossil occurrences. Waage (1979) postulated that such a stem-group probably resembled a glossinid-like ancestor in which one lineage subsequently became a nest-associate of birds and ruminant mammals (Hippoboscidae) and a second lineage became guano-feeding cohabitants with bats in cave habitats (Nycterbiidae + Streblidae).

Previous Designations. The mouthpart type discussed in this section traditionally has been included in the "dipteran mouthpart type" which in this study is considered the Labellate Mouthpart Class (Section 8.5.3). A reason for this lack of recognition of the distinctiveness of tubulostylates may be the scarcity of comparative material from the four constituent ectoparasitic families. However Jobling, in a series of articles (1926, 1928a, 1929, 1933), provided excellent descriptions of mouthpart structures from taxa of all four families. Matsuda (1965) reviewed some of Jobling's studies in his memoir on insect mouthparts and in 1969 James and Harwood defined a "fifth subtype: the sheep ked" within their "dipteran mouthpart type" (Table 6). In their treatise on hexapod mouthparts Denis and Bitsch (1973) considered *Pupipares* as a distinctive mouthpart theme of the Diptera. Discussions of *Glossina* mouthparts was provided in subsequent reviews, although both Smith (1985) and Chaudonneret (1989b) considered *Glossina* as a variant of muscid mouthparts that possess rasping, prestomal teeth.

Because of the characteristic, tubular piercing structure of the glossinid and pupiparian labellum, I consider the term **tubulostylate** an apt and meaningful descriptor of the most conspicuous and interactive mouthpart element in this mouthpart class. To my knowledge, this is the first introduction of the term.

Review of Literature. Considering the relative lack of taxonomic diversity in the tubulostylate mouthpart class, there has been ample doucumentation of mouthpart structures not only from each of the four taxonomic families, but also several genera within some of the families. One of the first illustrations and discussions of tubulostylate mouthparts was Hansen (1903) for *Glossina*. Subsequently, in a several excellent studies of mouthpart and head structure, Jobling discussed the hippoboscids *Lychnia maura* Bigot and *Melophagus ovinus* Linneaus in 1926, the nycteribiid *Cyclopoda sykesi* Westwood in 1928a, various streblids, including *Nycteribosca amboinensis* Rondani and *Raymondia lobulata* Speiser in 1929, and the glossinid *Glossina palpialis* Robineau-Desvoidy in 1933. Larger works that focused on dipteran external morphology and included data on head and mouthpart structure of tubulostylates included Peterson (1916) for the hippoboscids *Olfersia ardeae* Macquart, *M. ovinus* and various nycteribiids, Crampton (1942) for the hippoboscid *Ornithactona* and the nycteribiid *C. sykesi*, and Snodgrass (1943) for *G. palpialis*, *Lychnia americana* (Leach), *M. ovinus* and a nycteribiid. Scanning electron microscope studies of mouthpart structure include Popham and Abbdillahi (1975) for *Glossina morsitans* Vanderplank and Elzinga and Broce (1986) for three species of *Glossina* , four species of hippoboscids and one streblid. General reviews of mouthpart structure can be found in Matsuda (1965), Denis and Bitsch (1973), Smith (1985) and Chaudonneret (1989b).

8.9.10. Siphonostylate Class (Class 32)

Description. Head quadrate or transversely-elongated; proboscis very long. Genae moderately to minimally developed; gula present and well-developed, or absent. Antennae pectinate or filiform; ocelli absent; compound eyes expansive. Mouthparts hypognathous, stylate-haustellate, monostylate and retractile. Food pump clypeal and pharyngeal.

Clypeus quadrate and fused to frons. Labrum quadrate, undivided, a stylet-guide. Hypopharynx absent; epipharynx membranous. Mandibles absent. Maxilla with stipes elongated; lacinia and palpus absent. Galeae conjoined, a stylate siphon. Labrum with main-body elongated; glossae and paraglossae absent. Labial palps 3-segmented, penicil late and long. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. The principal structural feature of the Siphonostylate Mouthpart Class is the presence of a galeal siphon modified into a stylate structure for piercing resistant integument. Additionally there is the combination of the absence of many mouthpart elements (mandibles, maxillary palps, laciniae, glossae and paraglossae) and the presence of a well-developed, three-segmented, scaled labial palp.

Siphonostylates resemble siphonates (Section 8.6.2) although they are differentiated from them by the presence of a galeal, stylate siphon and the complete absence of certain mouthparts that are generally present as stubby features in siphonates. There is superficial similarity between the proboscides of siphonostylates and tubulostylates (Section 8.9.9), although the latter possesses a diagnostic tubulate stylet that is derived from the labium rather than maxillary galeae.

Diversity and Natural History. One of the more unusual and surprising modifications of insect mouthparts has been the conversion of the lepidopteran galeal proboscis from a sucking tube to a piercing implement capable of penetrating plant and animal integument. Such a structural modification is the basis of the Siphonostylate Mouthpart Class, which consists of medium- to large-sized noctuid and satyrid moths (the latter not examined in this study) with prominent galeal stylets generally about 2.5cm long (Butticker 1962).

Siphonostylates occur on various commercially- and naturally-grown fruits throughout the tropics (Golding 1945) and "semiparasitically" on various domesticated and feral ungulates in Southeast Asia (Bänziger 1986), thus imbibing fruit juices and blood as a group (Fig. 122). Siphonostylate mouthparts comprise a taxonomic diversity of two

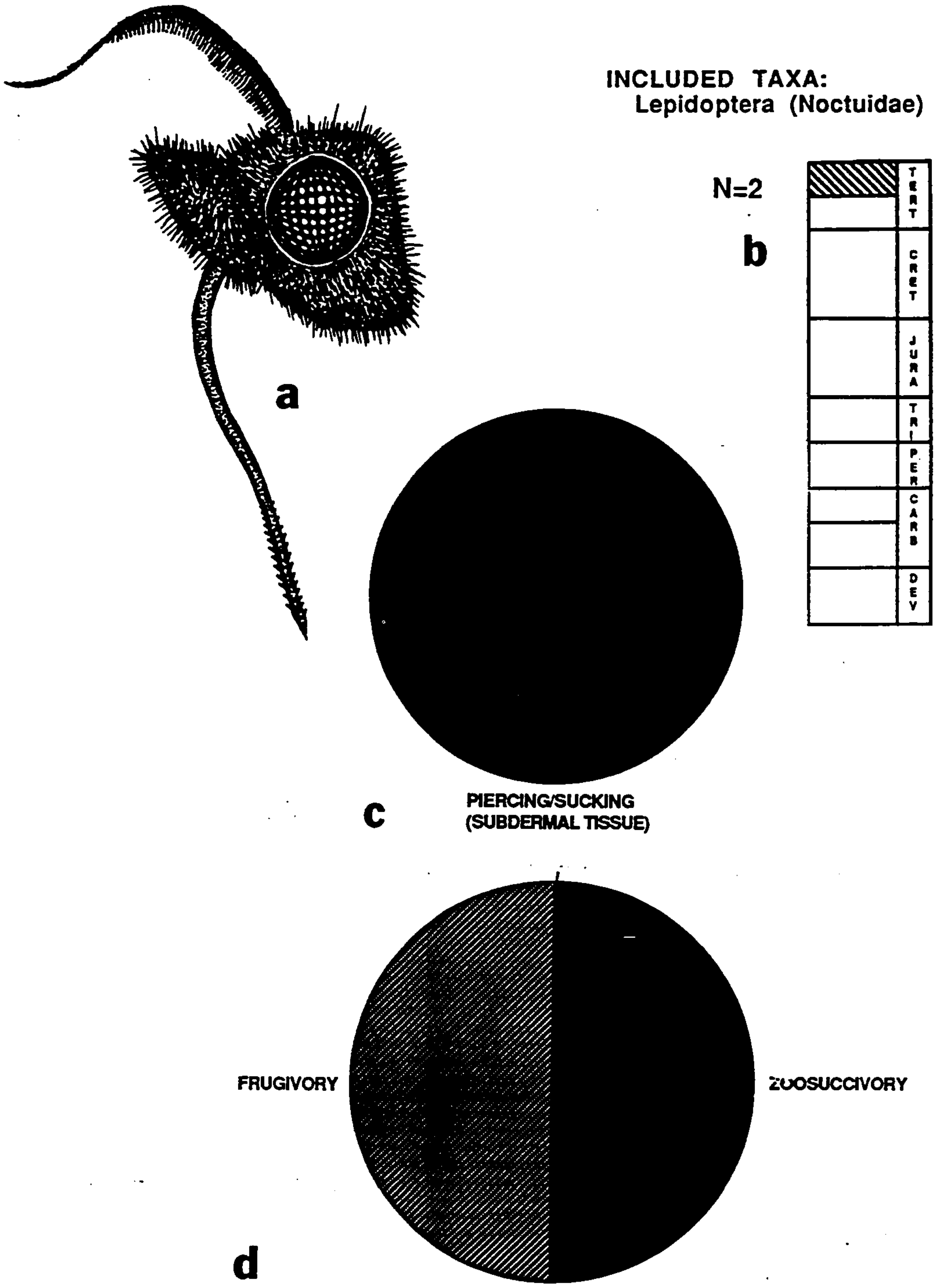


FIGURE 122. Overview of the Siphonostylate Mouthpart Class. a, *Calyptra orthograpta* Butler (Lepidoptera: Noctuidae, data-set no. 1219), after Bänziger (1979); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-group; d, dietary spectrum.

families, about 55 genera and about 200 species (from Buttiker 1962; Cochereau 1974, 1977; Bänziger 1982). Because of the occurrence of siphonostylates in regions with poorly known insect faunas, undoubtedly many more species exist; the head and mouthpart structures of only two species have been adequately described (Srivastava and Bogawat 1969; Bänziger 1970, 1980). Siphonostylates are the least diverse of the 34 mouthpart classes examined (Table 5, Fig. 131), and play a minor role in terrestrial ecosystems when compared to other more abundant groups. Nevertheless siphonostylate diversity is certainly underrepresented compared to other more diverse mouthpart classes. It is suspected that there is a high degree of structural mouthpart convergence within the class. Among ditrysan lepidopterans, satyrids and noctuids represent two independent originations from siphonate ancestors and, within the diverse Noctuidae, fruit- and vertebrate-piercing lineages have arisen at least several times. Because of the dearth of data on noctuid cladistic relationships, more data on the extent of convergence within siphonostylate mouthparts is unavailable.

The piercing mechanism of vertebrate integument by a stylate galeal siphon has been described by Bänziger (1970, 1971, 1980) and reviewed by Smith (1985) and Chaudonneret (1986). Bänziger (1980) described a four-step process of stylet penetration and withdrawal from vertebrate integument, commencing with antiparallel movements of the two galeae that impart a sawlike, scissors motion for cutting into a surface depression or weak spot on the skin. This action is combined with a rotatory motion of the proboscis for enhancing abrasion of the integument. Second, once limited penetration is achieved, galeal tearing hooks grip the skin to allow anchoring for further penetration by the antiparallel movements described above. Third, after the proboscis has sufficiently penetrated the hole, hydrostatically erect, retrally-directed barbs allow each galea to alternately slide past each other as the counterpart galea is anchored to tissue, allowing for advancement of the galeal siphon into deeper tissue. Finally withdrawal is achieved by relaxation of hemocoelic pressure and loss of barb erectness, with concomitant retraction of the galeal siphon as the hooks and barbs are directed distally. The basic mechanism for fruit-piercing siphonostylates appears similar (Srivastava and Bogawat 1969). In both cases the siphon is rigid and relatively long during penetration and bears a terminal armature of hooks and barbs. Initial puncture is accomplished by a thrust of the siphon onto the integument by a jerk of the head. Several structural modifications to withstand the structural forces experienced by a siphonate proboscis during feeding are known. They include placement of the siphonal "knee bend" close to the head and thus allowing for a longer uninterrupted segment of the siphon for increasing the impact force to the siphon tip, strengthening of the siphonal attachment region to the head, and enhanced efficiency of the fronto-clypeal pump (Srivastava and Bogawat 1969, Smith 1985).

The documented diet of fruit-piercing moths is principally commercially-grown fruit crops such as mango, guava, banana, longan, papaya, grape and tomato (Buttiker 1962, Bänziger 1982). The diversity of fruit-piercing species can be high locally: 88 species were recorded from Ghana (Golding 1945) and 86 species from Thailand (Bänziger 1986). Apparently only ripe fruit is attacked and fruits with very tough integuments or with lactiferous substances (e.g. Euphorbiaceae) are avoided. The degree to which naturally-occurring fruits are consumed and the host-specificities on particular fruit-producing species is not well known.

Siphonostylate feeding on ungulate blood is better documented, with most research being conducted on *Calyptra eustrigata* Hampson in Southeast Asia. This species apparently does not pierce healthy hide, but will attack weakened dermal areas, such as healing skin lesions, scabs and wounds (Bänziger 1986). *C. eustrigata* will attack the Indian elephant, Malagasy tapir, pig, buffalo and zebu. Although there is no evidence of *C. eustrigata* attacking normal, healthy vertebrate skin in nature, it readily penetrates the healthy skin of pig ear and the human finger under artificial conditions (Bänziger 1986). Although the Indian elephant is the "preferred" host of *C. eustrigata*, there is no indication of an obligate or even an evolving relationship since all native and introduced ungulates are attacked when available. At least four species of *Calyptra* are known to attack ungulates for blood in Southeast Asia. Unlike other sanguinivorous insects, only males have been observed to take up blood, and it is strongly suspected that females are fruit sap feeders (Bänziger 1986). Bänziger (1986) concluded that the blood meal of *Calyptra* males does not fulfill their nutritional requirements and that they probably imbibe fruit sap as well. Apparently all other species of *Calyptra* pierce fruit and are obligate frugivores. The presence of congeneric fruit-piercing and vertebrate skin-piercing species may not indicate a drastic dietary shift since ripe fruits attacked by many fruit-piercers produce fetid odors similar to decomposing animal

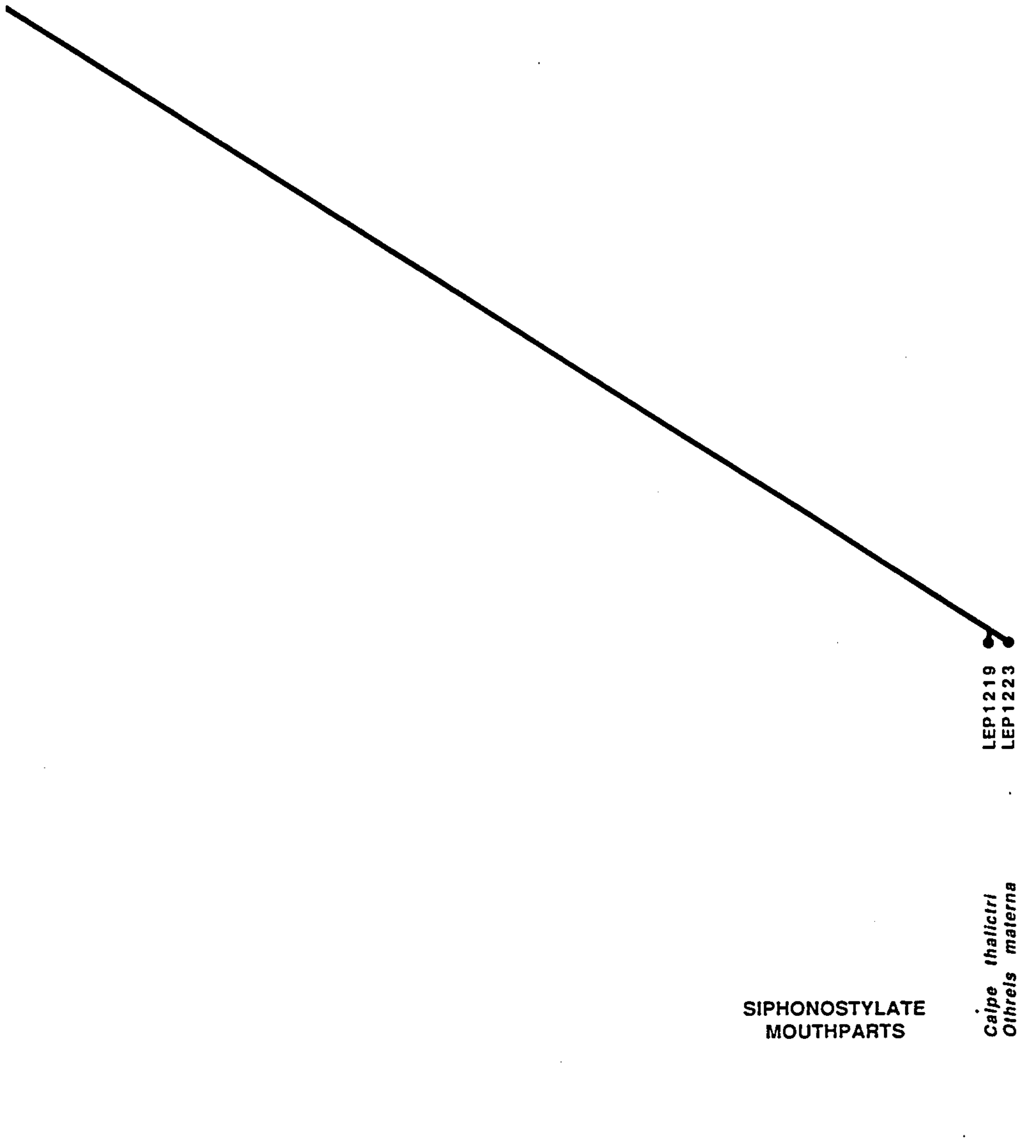


FIGURE 123. Cluster analysis dendrogram of taxa comprising the Siphonostylate Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

matter and include amino acids also found in animal tissues (Bänziger 1980).

Structural Themes. There are no structural themes evident in the dendrogram of siphonostylate mouthparts (Fig. 123).

Geochronologic History. Siphonostylates lack a fossil record. Although three fossil occurrences (Fig. 124) are attributed to noctuids --an egg from the Upper Cretaceous of Massachusetts (Gall and Tiffney 1983) and body fossils and leaf-mines from the Late Tertiary (Kozlov 1988)--it is impossible to determine whether they are from siphonate lineages (more likely) or siphonostylate lineages (less likely). Since there is undoubtedly considerable structural convergence upon the siphonostylate condition, a phenomenon that has occurred at the generic level seemingly at random in three noctuid subfamilies, even assignment of a potential noctuid fossil to a subfamily or tribe is insuffecement for placement in the siphonostylate class. Although the Noctuidae probably diverged from their sister-group, the Agaristidae, sometime during the Cretaceous (after Kozlov 1988), nothing can be concluded regarding the origin of noctuid subfamilies.

The only evidence available to base a tentative judge ment regarding the antiquity of the siphonostylate mouthpart class is the biogeographical distribution of various fruit and vertebrate skin-piercing species in Southeast Asia. According to Bänziger (1986) the vertebrate skin-piercing habit originated prior to 15,000yr BP when an exposed land bridge of continental shelf with a few minor water gaps connected New Guinea to the Asian mainland. If fruit-piercing is

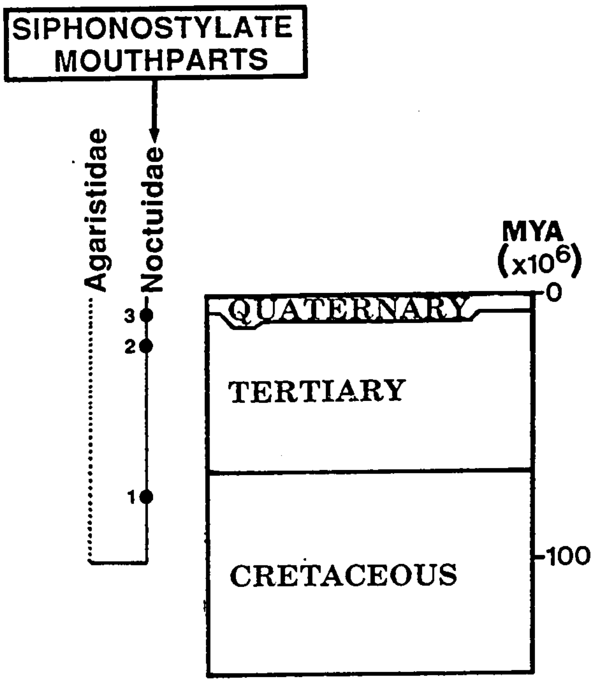


FIGURE 124. Geochronologic history of the Siphonostylate Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. Phylogram after Kozlov (1988b). The level of taxonomic analysis is the family. The outgroup is Agaristidae, which lacks a fossil record. Siphonostylates comprise several documented extant genera within the Noctuidae, and their fossil history is unknown; this phylogram indicates a maximum value for the geochronology of the mouthpart class.

ancestral to vertebrate skin-piercing, then the fruit-piercing habit is minimally Late Pleistocene in origin, possibly older.

Previous Designations. The first mention of lepidopteran proboscides that were structurally modified for penetration of integument was for the fruit-piercing *Ophidoderes fullonica* Linneaus by Darwin (1875) and Kückel (1875). Breitenbach (1882) later discussed the structure and function of barbs and hooks from the termini of various proboscides of fruit-piercing moths. Although Bänziger (1967-1986) and Srivastava and Bogawat (1969) discussed and illustrated the structure, feeding mechanism and nutritional ecology of several fruit and vertebrate skin-piercing moths, no designations were used to refer to this distinctive modification of the lepidopterian galeal siphon. (See Table 6 for a brief history of mouthpart nomenclature.) Because of the phenetic distinctiveness of this mouthpart type, I am using the term **siphonostylate** to convey both the structure of the proboscis as well as its role in obtaining fluid food from unexposed, tissue-bound fluid food.

Review of Literature. Early recognition of the stylate nature of certain lepidopteran proboscides can be found in Künckel (1975), Darwin (1875) and Breitenbach (1882). Descriptions of head and mouthpart structure were later provided by Srivastava and Bogawat (1969) for *Othreis materna* (Linneaus) and Bänziger (1970, 1971, 1980) for *Calyptra eustrigata* (Hampson). Regional inventories of fruit-piercing moths include Golding (1945) for Ghana, Buttiker (1962) for prominent tropical species and Bänziger (1982) for Thailand. Superb field work on the ecology of food procurement and feeding by skin-piercing moths on ruminants can be found in several works by Bänziger (1967, 1975, 1979, 1986). General, brief reviews of siphonostylate mouthpart structure are provided by Smith (1985) and Chaudonneret (1986).

8.10. Agnathate Series

8.10.1. General Features of the Agnathate Series

General Structure. The Agnathate Mouthpart Series is a taxonomicaly diverse assemblage of insects from seven orders (Ephemoptera, Homoptera, Coleoptera, Strepsiptera, Diptera, Lepidoptera and Hymenoptera) that are placed in two mouthpart classes (Reduced Trophic and Nontrophic) and are united by the shared property of highly reduced to virtually nonexistent mouthparts. Thus the members of the mouthpart series exhibit mouthpart reduction to a significant extent, and beyond the occasional absence of isolated mouthpart elements that are consequences of fusions, absences or modifications that, in part, define the unique mouthpart complexes of other mouthpart series. For example, while the Segmented Beak Mouthpart Class lacks important labial and maxillary elements, it nevertheless is characterized by the *presence* of an unique mouthpart organ--the hemipteroid beak. By contrast agnathates not only lack mouthpart elements to varying degrees and in varying mouthpart regions, they are additionally characterized by the *absence* of any substituted mouthpart organ.

Agnathates are either ephemeral nonfeeding adults or they are larval parasites or parasitoids that require few mouthpart elements for sustenance. Usually only one or at most a few mouthpart regions are demonstrably developed. Although the term "agnathous" is inexact for describing those forms with functional mandibles, the absence of other gnathal mouthpart elements in adjacent mouthpart regions from the same forms renders this term appropriate. Thus agnathate refers to any member in this series which exhibits some degree of major gnathal reduction, regardless of whether this reduction occurs in the mandibular, maxillary, labial or some other mouthpart region. Agnathates can be considered as a mouthpart group united more by the absence of structures than by the common possession of a functional, specific mouthpart organ. The term "agnathate" was previously used as a synonym for the order Plecoptera (Martynov 1930), presumably because of the trend toward mouthpart atrophy in adult plecopterans.

Mouthpart reduction has apparently affected the labial region most severely in agnathates, followed successively by the maxillary and labral regions. The mandibular region is the most persistent mouthpart region and remains present in many groups (Murphy 1922, Janvier 1933, Kinzelbach 1966) even though often there is no indication that the rudimentary mandibles are functional. This general reduction in mouthpart size is also associated with desclerotization, asymmetry and lack of shape constancy. Frequently there is great phenotypic variation in mouthpart development of forms with vestigial mouthparts (Needham, Traver and Hsu 1935).

Included Classes. Thie Agnathate Series comprises the Reduced Trophic and Nontrophic Mouthpart Classes (See table 6 for taxal membership, life-stages and number of taxa examined).

Diversity and Other Distributional Patterns. The Agnathate Series comprise a taxonomically diverse assemblage of adult and immature life-stages that occur in a variety of terrestrial habitats. They are either free-living, nonfeeding forms or are obligately coevolved larval parasitoids on other arthropods that have major effects on their arthropod hosts. Adult members of this mouthpart series are not involved directly with herbivory or pollination of vascular plants, unlike almost all other mouthpart series. However aphagy and concomitant mouthpart reduction may be a consequence of angiosperm colonization by holometabolous clades whose larvae function as the trophic stage, with subsequent relegation of the adult stage to an ephemeral, reproductive role only (partly from C. Finch, pers. comm.). Examples of adult aphagy in Holometabola originate principally in those clades that are leaf-miners, external-feeding caterpillars, and endoparasitoids. When compared to other mouthpart series agnathates are not exceptionally diverse at the species level; five of the seven other mouthpart have species diversities from two to over ten times that of agnathates. Much of this lack of series-level diversity is attributable to a dearth of documentary data for insects that have major mouthpart reduction.

The diets (or lack thereof) of agnathates constitute two major patterns. One group includes adults of male coccoids and strepsipterans, some zygaenoid lepidopterans and various unrelated dipterans which apparently do not feed as adults and frequently lack mouths or alimentary structures essential for the digestion of food. It is however unclear whether certain of these rare lepidopterans and dipterans with vestigial mouthparts feed, or whether they imbibe fluid food and thus are undocumented feeders due to the inadequacy of available ecologic data. By contrast the second group are principally larval or neotenic adult forms that are parasitoids of arthropod (mostly insect) hosts and have a diet of fluidized host tissue. The parasitoid strategy of not immediately killing their host upon entry or attachment serves to conserve food resources until a timely change in parasitoid life-stage, such as pupation or adult emergence.

Major Structural Variations. Two major structural themes occur within the Agnathate Mouthpart Series: the Reduced-Trophic and Nontrophic mouthpart classes. Fig. 28 illustrates the phenetically disjunct nature of these two themes. The Nontrophic Class exhibits sufficient similarity in head shape, sensory organ development and, to a lesser extent, mouthpart structure with a siphonate/haustoriate group (Sections 8.6, 8.5.2) that they share the same larger cluster. A distinctly different pattern is evident for reduced-trophics, which display the greatest degree of similarity with the three mandibulo-caniculate mouthpart classes (Section 8.4). Because of the presence of a basic holometabolous larval head structure with reduced mouthpart elements, strepsipterans and larval hymenopterans of the Reduced-Trophic Mouthpart Class exhibit their greatest similarities with the Mouthhook Class (Section 8.4.4) and, to a lesser degree, the Fossate-Complex and Tubulomandibulate Classes. Since mouthpart series assignments of mouthpart classes are based on functional criteria, the placement of two phenetically distant mouthpart classes in the Agnathate Series indicates that, while mouthpart reduction has occurred in numerous lineages, they can be described phenetically by two basic themes.

Geochronologic Range. Of the taxa examined in this study, major mouthpart reduction appears to be a Middle to Late Mesozoic phenomenon (Figs. 127, 130). However, because of the ubiquity of mouthpart reduction series among diverse, unrelated insect lineages, earlier instances of this phenomenon can not be ruled out and in fact are likely. It would be difficult to detect Paleozoic or Early Mesozoic reduced-trophics by an examination of the relevant insect fossils. Furthermore, because of the taxon-specific nature of mouthpart reduction, extrapolation of this mouthpart type to more inclusive taxonomic units is not advisable. This is particularly true for extant nontrophic ephemeropterans, whose Paleozoic ancestors had well-developed mandibulate mouthparts (Kukalová-Peck 1985). Thus the geochronologic range of agnathates incurs special problems inherent in the nature of a grouping based on a widespread phenomeon within in sects, rather than the origin of a particular discrete structure (or structures) that is more amenable to tracking through geologic time.

8.10.2. Reduced-Trophic Class
(Class 33)

Description. Head of variable shape, mostly free but commonly a cephalothorax, retractile or nonretractile; proboscis absent except in a few forms as a short process. Genae variable, often expanded dorsoventrally; gula variable, absent to prominently developed. Lorum absent; frontal/vertical region delineated and present, rarely absent. Antennae mostly absent to stubby, when well-developed filiform or lamellate/ flabellate, rarely otherwise; ocelli mostly absent, infrequently 2 and rarely more than 3 in number; compound eyes variable. Mouthparts reduced significantly in all forms to almost absent. When present mouthparts are mandibulate and placement is hypognathous or prognathous; food pump absent or present.

Clypeus mostly absent; when present quadrate to less commonly transversely-elongate in shape and undivided or fused to other structures. Labrum generally absent; when present shape is quadrate to transversely elongate, undivided or fused to clypeus; margin curvilinear, rarely otherwise. Hypopharynx and epipharynx mostly absent. Mandibles frequently absent; when present dicondylic, short-hooklike to ensiform or falcate, edentate, weakly musculated by adduction/abduction. Maxillae mostly absent; when present the main-body is single and equant and a palpus is present. When present, palpus generally 2- or 1-segmented, filiform to stubby or mucronate and often short, rarely long. Galeae and laciniae rarely present; when present usually generalized and spatulate. Labium frequently absent; when present main-body is generally elongate and undivided and bearing palpi or a labellum as appendages. Labial palps, when rarely present 1-segmented, mostly stubby and short. Glossae and paraglossae not evident. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. It is difficult to extract a consistent theme for a taxonomically heterogenous mouthpart class that is characterized more by the absence of structures rather than the possession of an unique mouthpart organ or an unique combination of mouthpart structures. The principal feature uniting members of the Reduced-Trophic Mouthpart Class is the *absence* of at least *one* major mouthpart region wherein at least 75% of the mouthpart regions is characterized by missing elements. Stated another way, reduced-trophics are diagnosed by the complete or near-complete absence of at least one major mouthpart region (labral, mandibular, maxillary or labial) or the absence of any combination of these regions. For example, whereas strepsipterans lack only about 75% of their labial mouthpart elements (one extreme), adult male coccoids are bereft of the labral, mandibular, maxillary and labial regions altogether (other extreme).

Two other mouthpart classes can be confused with reduced-trophics: segmented-beaks (Section 8.9.2) and the nontrophics (Section 8.9.3). Although segmented-beaks exhibit considerable reduction of mouthpart elements particularly from the maxillary and labial regions and are essentially apalpate, they nevertheless bear prominent maxillary laciniae and a prominent, labially-derived haustellum, unlike reduced-trophics. Nontrophics by contrast possess mouthpart reductions like reduced-trophics but the distribution of these reductions are not systematic and pervasive for entire regions (except for mandibles) and generally affect only two or three elements per mouthpart region. The extent of mouthpart reduction in nontrophics is much less than for reduced-trophics; nontrophics have lost principally maxillary galeae and laciniae, labial glossae and paraglossae and often mandibles.

Diversity and Natural History. Members of the Reduced-Trophic Mouthpart Class are small, inconspicuous, often larviform parasites or parasitoids on other arthropods and less frequently surface fluid imbibers or aphagous (Fig. 125). Reduced-trophics often participate in coevolutionary associations between arthropods in terrestrial ecosystems, and comprise principally three taxonomic groups that are united by a common theme of supression in various degrees of maxillary, labial and frequently other mouthpart regions (Giliomee 1967a, Roskam 1982, Kathirithamby 1989). Reduced-trophics comprise six orders, 70 families, approximately 3450 genera and approximately 27,800 species of insects (Appendix D) and have a rank-order of 11 out of 34 mouthpart classes (Table 5, Fig. 131). This significant diversity is matched by a respectable geochronologic duration with various constituent taxa having origins during the first half of the Mesozoic.

The dominant constitutent taxa of the mouthpart class are (i) adult male coccoids, (ii) all life-stages of strepsipterans and (iii) the larval stages of Hymenoptera-Parasitica from the superfamilies Chalcidoidea, Proctotrupoidea and Ceraphronoidea. (A few members from other isolated clades are also present, such as certain families of coleopterans, dipterans and hymenopterans.) The first of these groups is aphagous whereas the latter two groups are endoparasitic and less commonly ectoparasitic on a wide variety of terrestrial arthropodan hosts (Frost 1959, Malyshev 1968, Kathirithamby 1989). This taxonomic composition indicates that the reduced-trophic condition has been arrived at from at least 11 major, independent lineages (Fig. 126),

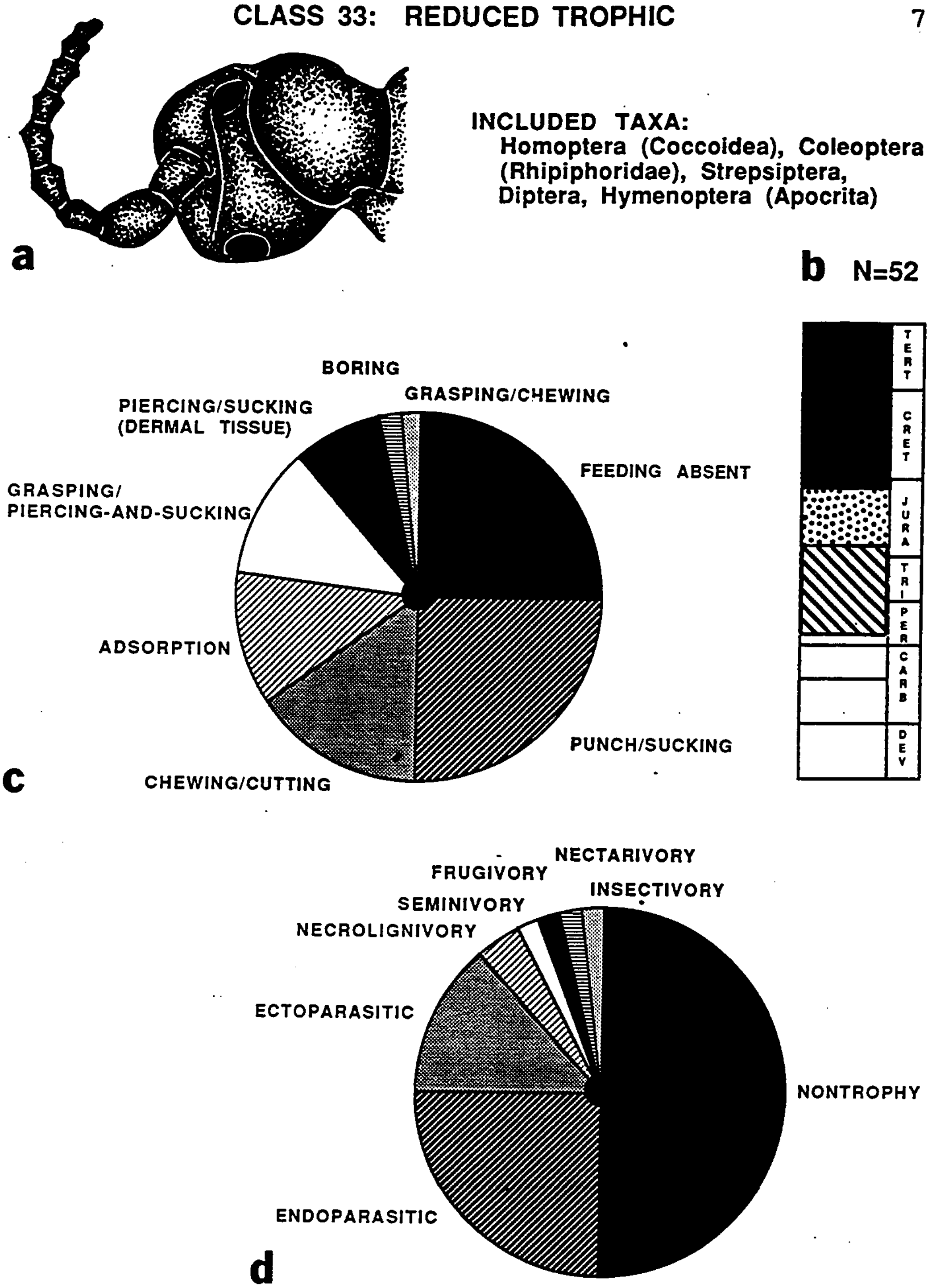


FIGURE 125. Overview of the Reduced-Trophic Mouthpart Class. a, *Apiomorpha ?pharetrata* (Schraeder) (Homoptera: Apiomorphidae, data-set no. 347), after Theron (1968); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

although the incidence of mouthpart reduction for insects (see also Section 8.10.3) is undoubtedly considerably higher. This is particularly true for holometabolous clades, wherein reduced mouthparts in the reproductive or adult stage and the frequent absence of feeding is a consequence of individual biomass acquired during the trophic or larval stage. For constituent larval parasites and parasitoids the reduced-trophic condition possesses the minimum complement of mouthparts necessary for securing an internal or external anchor to a host and for extraction of ambient host tissue for food. Almost always the mouthparts used for these functions are the mandibles; other mouthpart regions either bear rudimentary appendages or are bereft of appendages altogether. Of the three major groups mentioned above the Coccoidea and Strepsiptera are monophyletic lineages (Hennig 1981, Kathirithamby 1989); however a common ancestor currently can not be established for the three superfamilies (Proctotrupoidea, Chalcidoidea, Ceraphronoidea) of the Hymenoptera-Parasitica (Köningsmann 1978a). Thus additional convergences within the Reduced-Trophic Mouthpart Class may be present.

Most reduced-trophic members are liquid-feeders within host tissues, mostly by oral ingestion of fluidized food, but also by cutaneous assimilation. An exception to this dietary regime are adult male coccoids and strepsipterans, which bear vestigial mouthparts (Kinzelbach 1966, Richards and Davies 1977) and do not feed (Theron 1958, Kinzelbach 1969). Both groups are active fliers, although the hindwings of coccoids and forewings of strepsipterans are modified into halteres. They are also short-lived as reproductive adults, inseminating neotenic females devoid of wings, eyes and well-developed legs within hours of their emergence from a host (Bohart 1946b, Richards and Davies 1977). Other reduced-trophic members which do not feed include somatobrachyid and epipyropid lepidopterans and probably an agaonid parasitican hymenopteran (Fig. 125). Various unrelated dipteran groups such as adult nymphomyiids, acrocerids and gasterophilids have reduced-trophic mouthparts and are either aphagous or imbibe surface fluids.

Brues has characterized parasitoids, the dominant members of the Reduced-Trophic Mouthpart Class, in the following way:

> Some are clearly derived from predators, others from phytophagous ancestors, as nearly as we are able to judge on the basis of available criteria. Extreme specialization and convergence in both structure and development are commonly encountered throughout the entire series and this serves further to obscure the actual relationships between the numerous groups of the insects concerned (Brues 1972: 333).

Parasitoids are generally monophagous or oligophagous with respect to host species (Vinson and Barbosa 1987); few are polyphagous. Although they attack eggs, nymphs, larvae, pupae and adults of other insects, it is nymphs and larvae that are favored (Frost 1959). Host/parasitoid interactions can be distinguished from predation and parasitism by the predictability and temporal duration of the food resource. During growth and development predators are characterized by the immediate consumption of prey which fluctuates considerably in availability and variety; parasites consume a near-infinite host resource that is relatively unpredictable; and parasitoids consume a finite host resource that is relatively more predictable (Brues 1921, Vinson and Barbosa 1987). Parasitoids are perhaps best characterized as initially operating as a parasite by avoiding consumption of essential host organs and, before pupation, they kill the host akin to a predator (Frost 1959).

Parasitoidism among reduced-trophics involves a complex life-cycle in which one or more hosts are used by an internal or external larva to obtain nutrition without immediately killing the host. Among chalcidoids a broad spectrum of hosts are attacked, including taxa from virtually every holometabolous order, many hemimetabolous groups, thysanurans (silverfish), arachnids and mites (Gauld and Bolton 1988). Proctotrupoids are also endoparasitic and ectoparasitic, whose hosts include larval chrysopid planipennians (green lacewings), coleopteran larvae, dipteran pupae and nonspecific insect eggs. Ceraphronoids attack dipterans, coccoids, boreid mecopterans and neuropterans (Gauld and Bolton 1988). Strepsipterans also have a broad range of attacked hosts, including thysanurans, orthopteroids of at least four orders, homopterans, heteropterans, and a few major holometabolous groups (Kathirithamby 1989). In all these parasitoids a generalized life cycle commences with oviposition of an egg in or on a host followed by permanent attachment and feeding on nonvital host tissues by the hatched maggot. After a period of larval feeding the host is killed by the parasitoid as it consumes its vital organs. The remaining host carcass is frequently used as a substrate for parasitoid pupation. In most strepsiperans the female parasitoid is neotenically larviform in the host and is inseminated by the winged, free-living male through the host's body wall (Richards and Davies 1977). The resulting zygotes eventually hatch in the female strepsipteran's body cavity and are subsequently liberated into the host's body cavity where they undergo two or more structurally distinct larval stages. Such larval heteromorphy also occurs in parasitican hymenopterans, which are also characterized by supernumerary, distinctive larval stages (hypermetamorphosis).

An exceptional phenomenon occurring dominately in strepsipteran and parasitican hymenopteran parasitoids is obligate hyperparasitism. In hyperparasitism the larva of a parasitoid species in or on the primary host becomes, in turn, attacked by a second parasitoid species, eventually killing its newfound parasitoid host (Brues 1921, 1972; Kathirithamby 1989). Facultative hyperparasitism occurs when the secondary parasitoid larva has an option of either developing on the host or on the primary parasitoid species. One elaboration of this phenomenon is superparasitoidism, characterized by a complex biocoenosis of diverse parasitoids and parasites inhabiting a host, with numerous delete rious, neutral, or even beneficial associations occurring among the host inhabitants (Brues 1972, Kathirithamby 1989).

Structural Themes. Three dominant structural themes characterize the Reduced Trophic Mouthpart Class (Fig. 126). These themes are characterized by a morphological gradient in which forms with the greatest degree of missing mouthparts, principally adult male coccoids, are subclustered to the left of Fig. 126 and forms with the least amount of mouthpart reduction, namely all life-stages of strepsipterans, are subclustered on the right of the figure. The subcluster in the middle, parasitican hymenopterans, exhibit an intermediate level of mouthpart reduction. The single taxon *Schizaspidia tenuicornis* (data-set taxon 1288 in Fig. 126), a larval agaonid hymenopteran, is a fourth subcluster, but is unimportant in terms of the trend mentioned above.

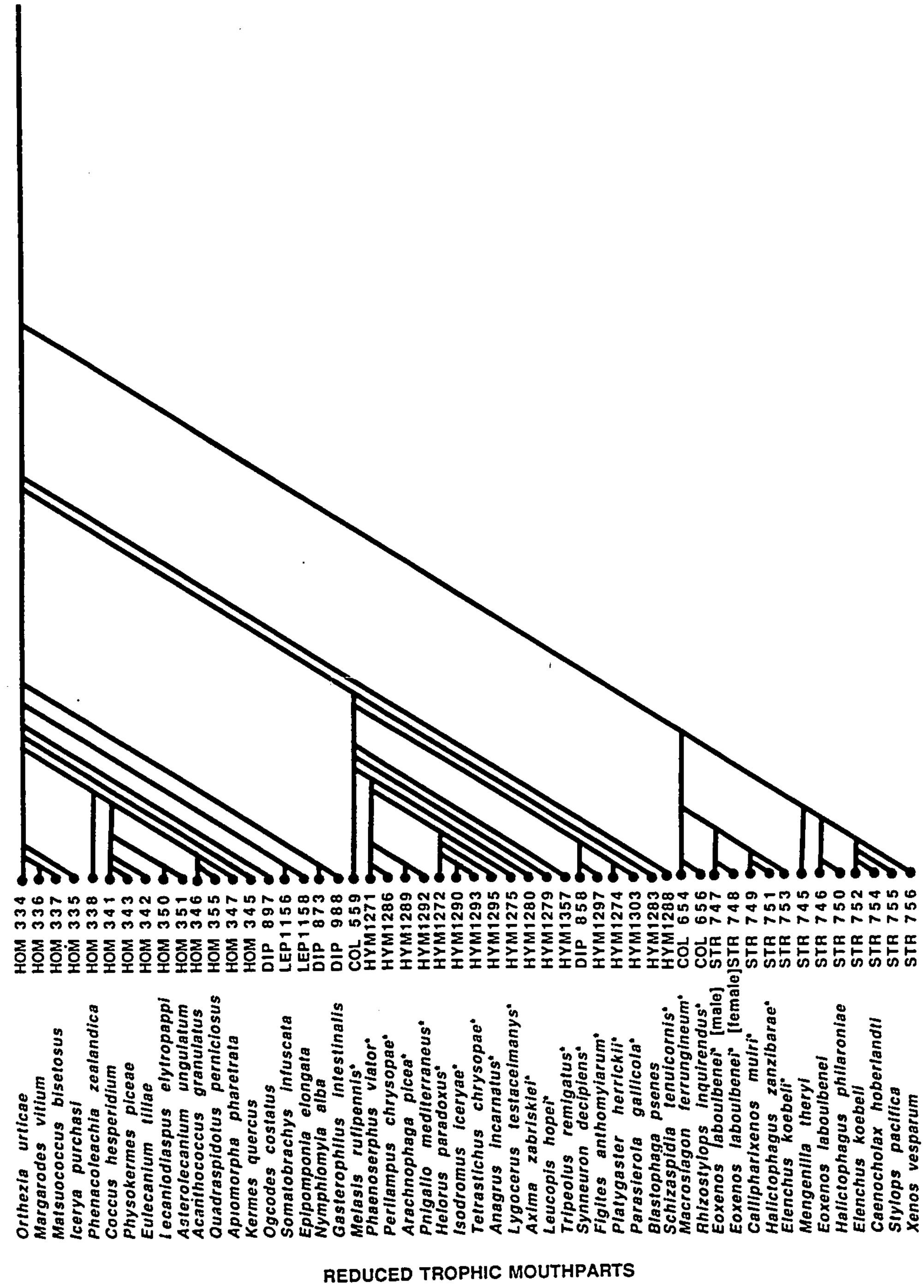

Orthezia urticae HOM 334
Margarodes vitium HOM 336
Matsuococcus bisetosus HOM 337
Icerya purchasi HOM 335
Phenacoleachia zealandica HOM 338
Coccus hesperidium HOM 341
Physokermes piceae HOM 343
Eulecanium tiliae HOM 342
Lecaniodiaspus elytropappi HOM 350
Asterolecanium ungulatum HOM 351
Acanthococcus granulatus HOM 346
Quadraspidotus perniciosus HOM 355
Apiomorpha pharetrata HOM 347
Kermes quercus HOM 345
Ogcodes costatus DIP 897
Somatobrachys infuscata LEP1156
Epipomponia elongata LEP1158
Nymphiomyia alba DIP 873
Gasterophilus intestinalis DIP 988
Melasis rufipennis* COL 559
Phaenoserphus viator* HYM1271
Perilampus chrysopae* HYM1286
Arachnophaga picea* HYM1289
Pnigalio mediterraneus* HYM1292
Helorus paradoxus* HYM1272
Isodromus iceryae* HYM1290
Tetrastichus chrysopae* HYM1293
Anagrus incarnatus* HYM1295
Lygocerus testaceimanys* HYM1275
Axima zabriskiei* HYM1280
Leucopis hopei* HYM1279
Tripeolus remigatus* HYM1357
Synneuron decipiens* DIP 858
Figites anthomyiarum* HYM1297
Platygaster herrickii* HYM1274
Parasierola gallicola* HYM1303
Blastophaga psenes HYM1283
Schizaspidia tenuicornis* HYM1288
Macrosiagon ferrugineum* COL 654
Rhizostylops inquirendus* COL 656
Eoxenos laboulbenei* [male] STR 747
Eoxenos laboulbenei* [female] STR 748
Callipharixenos muiri* STR 749
Halictophagus zanzibarae* STR 751
Elenchus koebeli* STR 753
Mengenilla theryi STR 745
Eoxenos laboulbenei STR 746
Halictophagus philaroniae STR 750
Elenchus koebeli STR 752
Caenocholax hoberlandti STR 754
Stylops pacifica STR 755
Xenos vesparum STR 756
REDUCED TROPHIC MOUTHPARTS

FIGURE 126. Cluster analysis dendrogram of taxa comprising the Reduced-Trophic Mouthpart Class. See Fig. 28 for relationship of this mouthpart class to other mouthpart classes.

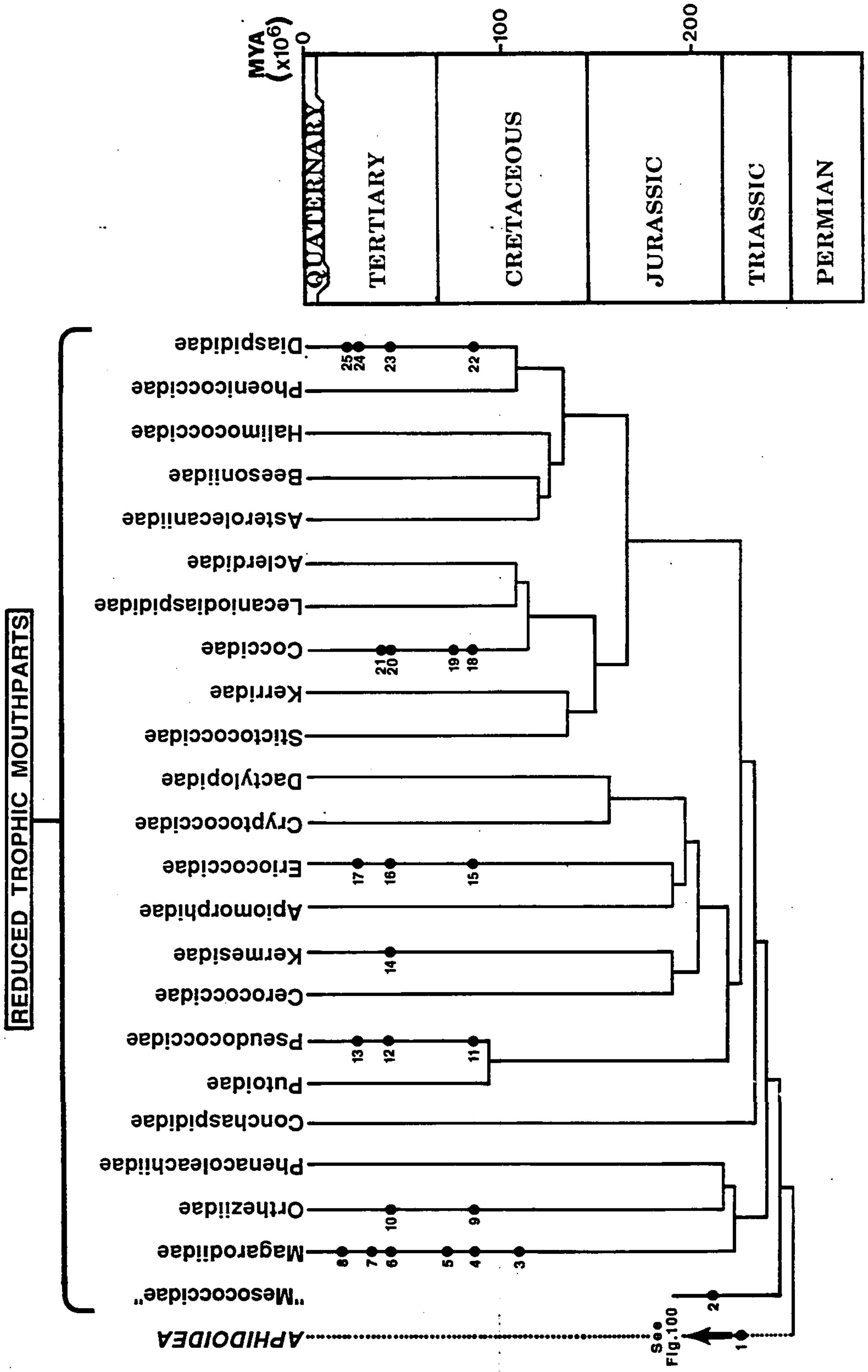
The subcluster dominated by adult male coccoids (data set taxa 334 to 345 in Fig. 126) and constituent segregates that include adult lepidopterans (1156, 1158) and dipterans (873, 988) exemplifies the greatest degree of mouthpart reduction for any taxa of the data-set. For some taxa of this subcluster up to 80% of all characters are represented as absent character-states, thus providing a distinctive quality to this group. For members of this subcluster, labra, epipharynges, hypopharynges, mandibles, maxillae and labia are missing. Thus male coccoids are ephemeral, nonfeeding forms that lack mouthparts and bear a minimum of sensory organs and head-related structures.

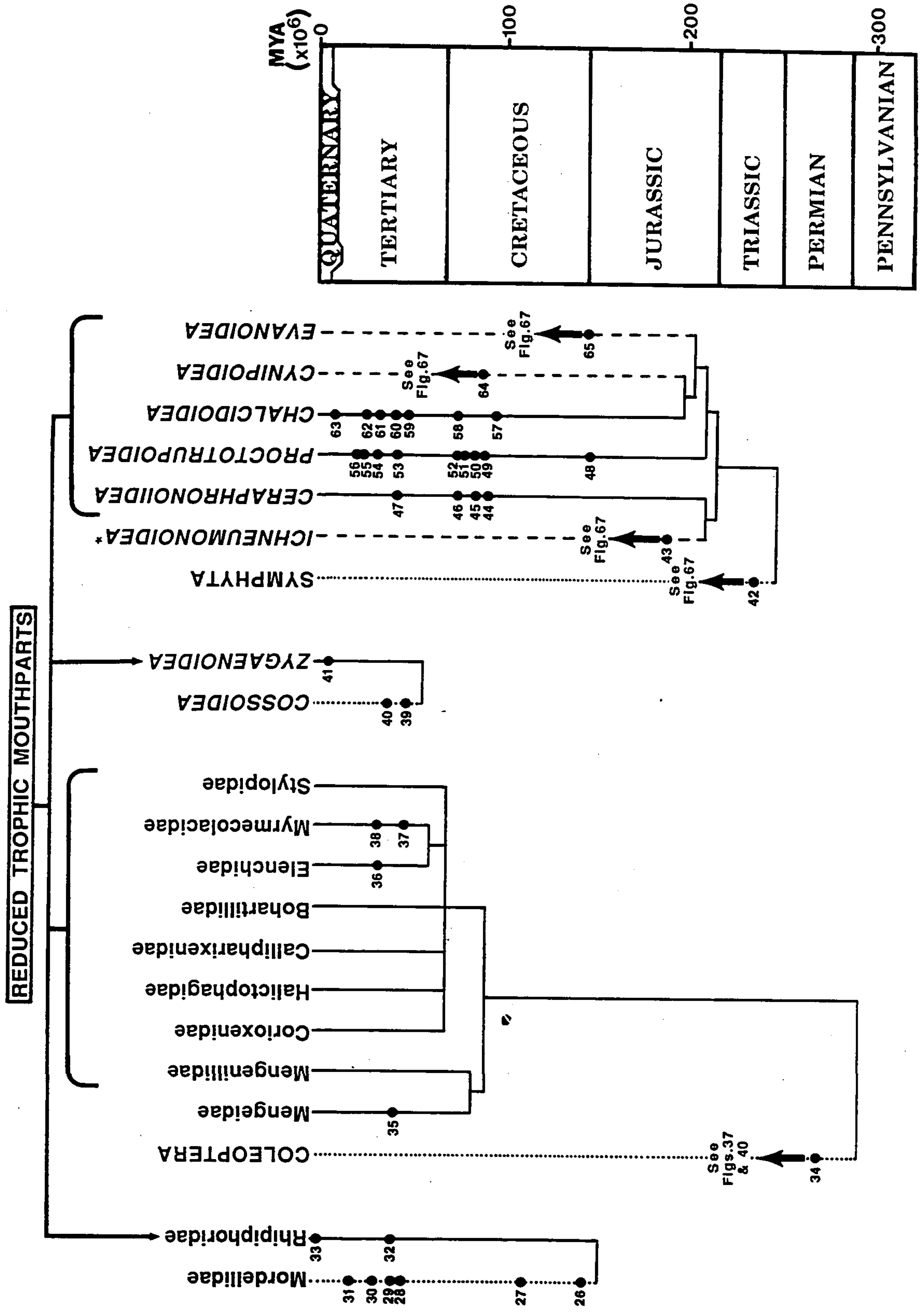
The subcluster located in the center of the dendrogram comprises members of three superfamilies of the Hymenoptera-Parasitica (1271 to 1283) and a single nematoceran dipteran (858). These taxa are characterized by absence of labra and maxillae, presence of mandibles and varying degrees of labial reduction that ranges from partial supression to complete absence. This characterization represents an intermediate condition between the extreme reduction of adult male homopterans and the modest reduction of the labium and often the maxillae found in rhipiphorid coleopterans (654, 656) and strepsipterans (747 to 756) in the subcluster at the right of Fig. 126. In the case of strepsipterans the labium is completely or near-completely absent and several elements of the maxillae are missing as well. When compared to adult male coccoids, mouthpart element absence has only affected about 20% of the 49 characters of a typical strepsipteran species.

Geochronologic History. In this section the fossil history of the three major and two minor taxonomic groups that contribute to the diversity of the Reduced-Trophic Mouthpart Class will be discussed. They are coccoid homopterans, strepsipterans, parasitican hymenopterans, rhipiphorid coleopterans and various dipteran groups. With the exception of diperans, phylogenies and fossil occurrences of these groups are provided in Fig. 127.

Although the isolated occurrence of *Mesococcus asiaticus* Bekker-Migdisova 1959 from the Late Triassic/Early Jurassic of the USSR [73] is an early exception, all known coccoid fossils are Cretaceous or Cenozoic in age and are referrable to extant families (Koteja 1986). Most of these fossils are adult alate males (Koteja 1986) and thus are comparable to Recent reduced-trophics. The earliest described coccoid is the margarodid *Eomatsucoccus sukachevae* Koteja 1988c from the Early Cretaceous of the USSR [52]. From Late Cretaceous amber of the USSR [37] a diverse fauna of margarodids, ortheziids, pseudococcids, eriococcids, coccids and diaspidids have been documented (Koteja 1986) and from somewhat younger Cretaceous Canadian amber [35] a margarodid and a coccid are known (Beardsley 1969). By mid-Tertiary times additional amber material indicates that many of the extant plant predator/host plant associations were in existence (Koteja 1988c). However Koteja (1985, 1988c) concludes, because of the occurrence of Early Cretaceous coccoids whose modern representatives are coevolved on gymnospermous hosts, that the Coccoidea experienced a major radiation onto various gymnosperms during the Jurassic. Only a portion of this fauna was

FIGURE 127. Geochronologic history of the Reduced-Trophic Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylograms are after Schlee (1969) and Koteja (1974) for Coccoidea, Crowson (1981) for Mordellidae + Rhipiphoridae, Kathirithamby (1989) and Hennig (1981) for Strepsiptera, Scott (1986) and Kozlov (1988b) for Zygaenoidea + Cossoidea, and Köningsmann (1978a) for nonaculeate Hymenoptera. The level of analysis is the family, except for the nonaculeate Hymenoptera and Lepidoptera, which are analyzed at the superfamily level. Outgroups are Aphidoidea for Coccoidea, Mordellidae for Rhipiphoridae, Coleoptera for Strepsiptera, Cossoidea for Zygaenoidea, and Symphyta for nonaculeate Hymenoptera. These fossil occurrences are not a complete inventory of all documented fossil members of this mouthpart class.


MYA
(x10^6)
0
100
200
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
Diaspididae
Phoenicococcidae
Halimococcidae
Beesoniidae
Asterolecaniidae
Aclerdidae
Lecaniodiaspididae
Coccidae
Kerridae
Stictococcidae
Dactylopidae
Cryptococcidae
Eriococcidae
Apiomorphidae
Kermesidae
Cerococcidae
Pseudococcidae
Putoidae
Conchaspididae
Phenacoleachiidae
Ortheziidae
Magarodiidae
"Mesococcidae"
APHIDOIDEA
See Fig.100
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
REDUCED TROPHIC MOUTHPARTS


MYA
(x10^6)
0
100
200
300
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
PENNSYLVANIAN
REDUCED TROPHIC MOUTHPARTS
EVANOIDEA
CYNIPOIDEA
CHALCIDOIDEA
PROCTOTRUPOIDEA
CERAPHRONOIDEA
ICHNEUMONOIDEA*
SYMPHYTA
ZYGAENOIDEA
COSSOIDEA
Stylopidae
Myrmecolacidae
Elenchidae
Bohartillidae
Callipharixenidae
Halictophagidae
Corioxenidae
Mengenillidae
Mengeidae
COLEOPTERA
Rhipiphoridae
Mordellidae
See Fig.67
See Figs.37 & 40
26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65

subsequently co-opted by angiosperms. A similar conclusion was made by Jarzembowski (1989) for aphids, the sister-group to coccoids. The actual origin of the Coccoidea + Aphidoidea was much earlier, probably during the Late Permian or Early Triassic (Hennig 1981).

The fossil history of strepsipterans is confined to the Cenozoic. The oldest form is a specialized myrmecolacid primary larva from the Eocene of Germany [24] (Kinzelbach and Lutz 1985). The younger Baltic amber fauna [19] also has yielded myrmecolacids and adult male specimens of the more primitive family Mengeidae (Ulrich 1927, Keilbach 1939). Recent mengeids possess a larval stage that is a parasitoid of a soil-inhabiting thysanuran rather than the more typical hymenopteran host (Larsson 1978). From Miocene Dominican amber [17] myrmecolacid and closely related elenchid specimens have been recovered (Kinzelbach 1979, 1983). In an evaluation of strepsipteran diversity and host/parasitoid specializations from these three deposits, Kinzelbach and Lutz (1985) have concluded that the Strepsiptera extends to the Jurassic and probably had an origin during the Permian. Kathirithamby (1989) did not venture a judgement regarding the timing of strepsipteran origin, but did note that the Eocene myrmecolacid larva was very apomorphic in structure.

Rhipiphorid larvae are structurally very similar to strepsipterans (Crowson 1981) and are members of the same subcluster of reduced-trophics (Fig. 127). They are often considered as convergent upon the strepsipteran ground plan (Kinzelbach 1971, Kathirithamby 1989) and thus not closely related. Rhipiphorids are documented from Upper Eocene/

Lower Oligocene Baltic amber [19] (Keilbach 1982) and from subfossil Burmese amber (Cockerell 1917) although their sister-group the Mordellidae is known from the Upper Jurassic of the USSR [60] (Crowson 1974, 1981). Accordingly rhipiphorids are presumed to have a Late Jurassic or somewhat earlier origin.

Various unrelated dipteran groups have independentaly undergone significant mouthpart reduction, including larval hyperoscleids and adult nymphiomyiids, acrocerids and gasterophilids. Nymphomyiids lack a fossil record (McKevan and Cutten 1981) although Rohdendorf (1974) and Rohdendorf and Kalugina (1974) consider them as a relict group of primitive Mesozoic-aspect flies belonging the once-diverse suborder Archidiptera. Although hyperoscelids are known from Upper Eocene/ Lower Oligocene Baltic amber [19] (Hennig 1964), the relevant constituent subfamily Synneurinae lacks a fossil record (Peterson and Cole 1981). Acrocerids are typical members of the monostylate/distylate mouthpart class and have fossil occurrences extending to the Upper Jurassic of the USSR [60] (Ussatchov 1968). Gasterophilids have a fossil record extending to the Paleogene (Rohdendorf 1974) and the abundant larval botfly deposits of *Lithophyoderma* from the Eocene of Wyoming [23] (Grande 1980) may be an example. (For the timing of origin of these groups or their more inclusive clades, see Figs 82, 109, 115).

The origin of the Hymenoptera-Parasitica (also known as Terebrantia or Heterophaga) appears to have been during the Middle Jurassic based on a cladistic analysis of Recent representatives (Köningsmann 1978a, Hennig 1981). Although there is considerable uncertainity regarding the origin of specific parasitican groups within the suborder Apocrita (Hennig 1981), isolated Jurassic and Cretaceous fossils can be assigned to particular Recent families or superfamilies. The earliest fossil hymenopteran is *Archexyela crosby* Riek 1955, a xyelid from the Upper Triassic of Queensland [74], but the earliest known parasiticans do not enter the fossil record until the Late Jurassic to Lower Cretaceous (Köningsmann 1978a). These parasitican fossils include *Ephialtites* (Evanoidea: Ephialtitidae) from the Upper Jurassic of the USSR [60] (Rasnitsyn 1975, 1980) and the Lower Cretaceous of Spain [56] (Meunier 1903, Whalley and Jarzembowski 1985). Additionally, Upper Jurassic evanoid, aulacid-like forms have been assigned to the Praeaulacidae and comprise at least eight genera from the same Upper Jurassic deposits [60] mentioned above (Rasnitsyn 1972).

Members of the three major reduced-trophic parasitican superfamilies--Proctotrupoidea, Ceraphronoidea and Chalcidoidea--are traceable to the Late Jurassic or earliest Cretaceous. The Upper Jurassic form *Mesohelorus machini* Martynov from the USSR [60] was once placed in the Proctotrupoidea (Rohdendorf 1962, Rasnitsyn 1980), although Hennig (1981) believed that it may equally be an aculeate. An unnamed proctotrupoid fossil has been documented from Lower Cretaceous deposits from southern Australia [53] (Jell and Duncan 1986). Proctotrupoid scleonids have been described from Late Cretaceous Canadian amber [19], where they comprise six species (Brues 1937). Additional Baltic amber proctotrupoids include diapriids and proctotrupids (Brues 1923, Larsson 1978). Members of the superfamily Ceraphronoidea, namely ceraphronids, have been recovered from Late Cretaceous Alaskan amber [40] (Langenheim et al. 1960), Late Cretaceous Canadian amber [35] (Muesebeck 1963, Carpenter et al. 1937) and Baltic amber [19] (Brues 1923). These three amber localities have also produced numerous chalcidoid fossils, including an eulophid from Alaskan amber (Langenheim et al. 1960); a tetracampid, trichogrammatid, mymarid and unidentified chalcidoid from Canadian amber (Carpenter et al. 1937, McAlpine and Martin 1969, Yoshimoto 1975); and a diverse assemblage of nine chalcidoid families from Baltic amber (Larsson 1978).

Telenga (1969) has presented a hypothesis for the origin of parasitism in the Hymenoptera-Parasitica based on relationships between parasitoid and host pairs among Recent representatives and on the phylogenetic proximity of primitive parasiticans to particular symphytan groups. He concludes that parasiticans arose from a siricoid-like symphytan and parasitized wood-boring buprestid and cerambycid coleopteran larvae. Malyshev (1968) presents a similar hypothesis but differs in advocating the initial predation and eventual parasitoidism by primitive parasitican lineages of symphytan larvae occurring in leaf galls. Much of the support for Malyshev's (1968) hypothesis comes from behavioral studies of symphytan and parasitican hymenopteran taxa.

Thus the geochronologic distributions of fossils representing major lineages of reduced-trophics indicates that this mouthpart class originated during the Late Permian to Early Triassic (coccoid homopterans) to Middle Mesozoic (parasitican hymenopterans). Strepsipterans probably had a Middle Mesozoic or even later origin, although arguments for a Permian origin may place strepsipterans among the earliest members of this class. The establishment of numerous host/parasitoid relationships in this mouthpart class has been associated with mouthpart reduction in several holometabolous groups.

Previous Designations. Descriptive terms such as "reduced-trophic" have not been used in the entomological literature for referring to a group (or groups) of hexapods exhibiting vestigial mouthparts, particularly if they are taxonomically unrelated. However references to mouthpart reduction have been made for selected taxa in specialized taxonomic accounts (e.g., Bohart 1946b, Hering 1951, Short 1952). An early attempt of more comprehensive consideration of mouthpart reduction throughout the class was by Metcalf et al. (1962) who recognized a "degenerate type" of mandibulate larval mouthpart design in hymenopterans and other larval groups, but did not mention rudimentary adult mouthparts (Table 6). An exception to this was the thorough monograph by Denis and Bitsch (1973: 41) on hexapod mouthpart structure, who considered mouthpart reduction in adult male coccoids, strepsipterans in general, and chalcidoids and proctotrupoids as examples of "*réduction des pièces buccales*" and worthy of recognition as a distinct type of mouthpart modification. Later, Chaudonneret (1983: 123) discussed under the heading of "*réduction des pièces buccales de type broyeur*" mouthpart rudimentation in adult male strepsipterans and coccoids, larval hymenopterans (especially parasitic forms), dipterans, adult ephemeroperans and some adult lepidopterans. Chaudonneret's (1983) discussion corresponds approximately to the Reduced-Trophic and Nontrophic Mouthpart Classes outlined in this study.

The general absence of recognition of a highly reduced mouthpart class by many authors is probably attributable to a perceived continuum of mouthpart structure between fully-developed and rudimentary phases within particular adult or larval mouthpart types. However these two "end-members" are discrete classes, as Fig. 28 indicates, and are associated with profound differences in diet and also major differences in head structure, sensory organ structure, and the presence or absence of labral, mandibular, maxillary and labial regions. Because of the distinctiveness of various taxa with rudimentary mouthparts, the term **reduced-trophic** is herein appropriated as a name.

Review of Literature. There are few classical descriptive treatments of the head and mouthpart structure of reduced-trophic species, probably because of the lack of sufficient mouthpart complexity to warrant a description. The only significant exception is Kinzelbach's (1966) extensive account of adult male strepsipteran mouthparts. The overwhelming bulk of documentation for head and mouthpart structure originated from extensive monographic accounts of the systematics of particular, often economically-important groups. In these accounts the head and mouthpart structure of representative taxa are discussed and illustrated, frequently in brief outline. This literature review will focus first on the data sources for the three major groups--adult male coccids, parasitican hymenopterans and strepsipterans, ending with a treatment of the minor groups.

Several major taxonomic and morphological accounts of adult male coccoids were used in the compilation of data in this study. Balachowsky's (1937) study of the external structure of many European coccoids, including the ortheziid *Orthezia urticae* Linneaus, the margarodiid *Icerya purchasi* Maskell, the coccid *Eulecanium tiliae* (Linneaus), the diaspidid *Parlatoria blanchardi* Targioni-Tozetti and the kerrid *Laccifer lacca* Kerr was a rich source of data, as was Russell's (1941) revision of the taxonomy of the asterolecaniid *Asterolecanium* sp. Ferris' (1955) compendium of coccoid morphology is a useful reference for the external structure of the families Acleridae, Asterolecaniidae, Conchaspididae, Dactylopidae and Kerridae. Jancke (1955) provided one of the earliest, in-depth studies of adult male coccoid morphology and supplied illustrations and discussions of external structure for many families, including the phenacoleachiid *Phenacoleachia zelandica* (Maskell), the pseudococcid *Pseudococcus citri* Risso, the coccid *Physokermes piceae* (Schrank), the kermid *Kermes quercus* Linneaus, the asterolecaniid *Asterolecanium ungulatum* Russell and the diaspidid *Quadraspidotus perniciosus* Comstock. Jancke's focus on adult male structure was followed by Theron (1958) who surveyed the external structure of many forms, including the margarodid *Margarodes vitium* Giard, *Pseudococcus adonidum* (Linneaus), the coccid *Eulecanium taxi* Habib and other forms. Lastly, Giliomee (1967a) additionally has documented male coccoid structure by adding the coccids *Physokermes piceae* (Schrank) and *Coccus hesperidium* Linneaus to the inventory of available taxa. More focused studies on one or two taxa include Giliomee (1967b) for the structure of the male lecaniodiaspidid

Lecaniodiaspis elytropappi Munting and Giliomee, Giliomee (1968) for a similar study of *Asterolecanium* sp., Beardsley's (1968) description of *Matsuococcus bisetosus* Morrison and Theron's (1968) account of the apiomorphid *Apiomlorpha ?pharetrata* (Schraeder).

Source documentation for strepsipterans of all life cycle classes comes from Pierce's (1918) and Bohart's (1946b) taxonomic revision of the Strepsiptera, with descriptions and illustrations of important life-stages of then-known species. Bohart (1943, 1946a, 1962) also described new species of *Halictophagus*. Parker and Smith (1933) provided a useful description of the mengillid *Eoxenos laboulbenei* Peyerimhoff. By far the most useful source was Kinzelbach's (1966) extensive documentation of the head and mouthpart structure of adult males from four families of strepsipterans.

Several major taxonomic accounts are available for the head and mouthpart structure of larval parasitican hymenopterans. These include Marchal's (1906) monograph on the Platygasteridae, including descriptions of external larval structure, and Silvestri's (1924) study of the natural history of oak parasitoids such as the bethylid *Parasierola gallicola* Kieffer, which occurs endoparasitically on an oak-feeding tortricid caterpillar. Grandi (1925) provided a taxonomic monograph on Indo-Malesian agaonids, including a description of the larva of *Blastophaga psenes* Linneaus. The cynipid parasitoids of dipteran larvae, including *Figites anthomyiarum* (Bouché) were detailed by Jones (1928), who used a natural-historical approach that was also found in Janvier's (1933) extensive account of Chilean hymenopterans, including a description of the larva of the leucopsid parasitoid *Leucopsis hopei* Spinola.

Finally, Clancy's (1946) monograph on hymenopteran parasitoids from larvae of chrysopid neuropterans was a valuable sorce of data for the helorid *Helorus paradoxius* (Provancher), the perilampid *Perilampus chrysopae* Crawford, the eupelmid *Arachnophaga picea* (Howard), the encyrtid *Isodromus iceryae* Howard and the eulophid *Tetrastichus chrysopae* Crawford. Shorter contributions, focusing on the external structure of one or two species include Haviland (1921) for two species of the ceraphronid *Lygocerus*, Hill and Emery (1937) for the platygasterid *Platygaster herricki* Packard, Jackson (1961) for a brief account of the proctotrupid *Phaenoserphus viator* Haliday and the mymarid *Anagrus incarnatus* Haliday, and Burks (1966) for the eurytomid *Axima zabriskiei* Howard.

Head and mouthpart data for minor reduced trophic groups--dipterans, coleopterans and lepidopterans--were available from several sources. For dipterans, the enigmatic nymphomyiid *Nymphiomyia alba* Tokunaga was described by Tokunaga (1932, 1935), the larval hyperoscelid *Synneuron decipiens* Hutson was detailed by Mamaev and Krivosheina (1969) and Teskey (1976), the gasterophilid *Gasterophilus intestinalis* DeGeer by Peterson (1916) and Cole (1969), and the acrocerid *Ogcodes* sp. by Peterson (1916), Crampton (1942) and Schlinger (1981). The rhipiphorid larvae of *Macrosiagon ferrungineum* Fabricius and *Rhizostylops inquirendus* Silvestri were documented by Grandi (1936, 1937, 1959) and Silvestri (1905) respectively. The zygaenoid lepidopterans *Somatobrachys infuscata* Klug and *Epipomponia elongata* Jordan were described by Jordan (1916, 1928) respectively.

8.10.3. Nontrophic Class
(Class 34)

Description. Head transversely elongate, nonproboscate. Genae moderately to minimally developed. Antennae setaceous, rarely pectinate; ocelli absent or 3; compound eyes expansive. Mouthparts hypognathous, generally nonfunctional, with asymmetry. Food pump usually absent.

Clypeus quadrate; labrum variously shaped, single, margin often straight to curvlinear. Hypopharynx absent, rarely a bulbous reservoir; epipharynx membranous or absent. Mandibles absent or rarely present (vestigial). Maxillae reduced, lacking laciniae, less commonly galeae. Maxillary palps short to vestigial, mostly functional; generally 1-segmented, rarely 2- or 3-segmented; stubby or brushlike. Galeae, when present, generalized and/or stubby. Labium elongated, mostly bearing functional palpi. Labial palpi penicillate or squamate; 1- or 2-segmented; short to rarely intermediate in length. Glossae and paraglossae generally absent. Interregional co-optation of mouthpart elements absent.

Key Phenocharacters. The Nontrophic Mouthpart Class is characterized by presence of prominent, well-developed sensory organs, a transversely-oriented head capsule and nonfunctional, rudimentary or absent mouthparts. The mandibles, laciniae, galeae, glossae and paraglossae are usually absent or rudimentary and, if present, are always nonfunctional. This is in stark contrast to large, expansive eyes and well-developed, conspicuous antennae of the mouthpart class.

This mouthpart class may be differentiated from adult ectognathates (Section 8.3.4) and pectinates (Section 8.3.11) by the absence of many mouthpart elements and presence of a transversely-oriented head with well-developed antennae and eyes. Nontrophics are differentiated from siphonates (Section 8.6.2), to which members of lineages included in the Nontrophic class belong, by absence or extreme reduction of the galeal siphon, laciniae and labial palps. Although reduced-trophics (Section 8.10.2) also possess a reduction of mouthpart elements, it differs from nontrophics by the presence of rudimentary sensory organs and complete absence of the labral, labial and often maxillary regions. Ironically, reduced-trophics are characterized by greater loss of elements but have members that are able to feed, whereas nontrophics have apparently undergone less mouthpart loss but are unable to ingest food.

Diversity and Natural History. Many holometabolous adults do not feed during the adult stage. For these taxa the adult stage is effectively a reproductive phase and is frequently ephemeral compared to the longer duration of the trophic larval stage. Thus many holometabolous insects store sufficient food reserves during the larval stage that, upon pupation, the adult does not require additional nutrition for sustaining a short, reproductive phase (Brues 1972). There are an estimated 5200 nontrophic species, representing 19 families of ephemeropterans and three families of lepidopterans (Appendix D), placing nontrophics in a rank-order of 20 out of 34 mouthpart classes (Table 5, Fig. 131). This figure is undoubtedly an underrepresentation since many adult lepidopterans did not enter the data-set because of the lack of source documentation. Nontrophics are nevertheless dwarfed percentagewise in the modern fauna by reduced trophics (Section 9.10.2) most of which are true feeders. No other mouthpart class has the degree of functional and structural mouthpart convergence as nontrophics. Although ephemeropterans have probably undergone mouthpart reduction once, holometabolous forms have undergone a profusion of mouthpart reduction series in numerous lineages. This is borne out in lepidopterans, in which many normally siphonate families have many unrelated genera with mouthpart reduction and aphagy (*vide infra*). Generally, the Nontrophic Mouthpart Class is insignificant in the food resource economy of modern ecosystems, almost by definition. It is the only mouthpart class that is not a member of a food-resource guild (Fig. 128).

An examination of several sources documenting the structure and lengths of lepidopteran proboscides from various families (Philpott 1927, Taylor 1957, Proctor and Yeo 1973, Willemstein 1987) reveals that at least one and frequently many genera in 33 families of lepidopterans bear nontrophic siphons that are very short, vestigial or rudimentary, or absent. Those families with nontrophic members were centered in the superfamilies Eriocranoidea, Neopseustoidea, Mnesarchaeoidea, Hepialoidea, Cossoidea, Zygaenoidea, Castnoidea, Pyraloidea, Bombycoidea and Noctuioidea, indicating a pervasive occurrence throughout the order. Thus complete to near-complete siphon reduction in lepidopterans is a commonplace feature, occurring not only in plesiomorphic and often mandibulate groups, but also in apomorphic groups with nominally long and functioning galeal siphons.

CLASS 34: NONTROPHIC

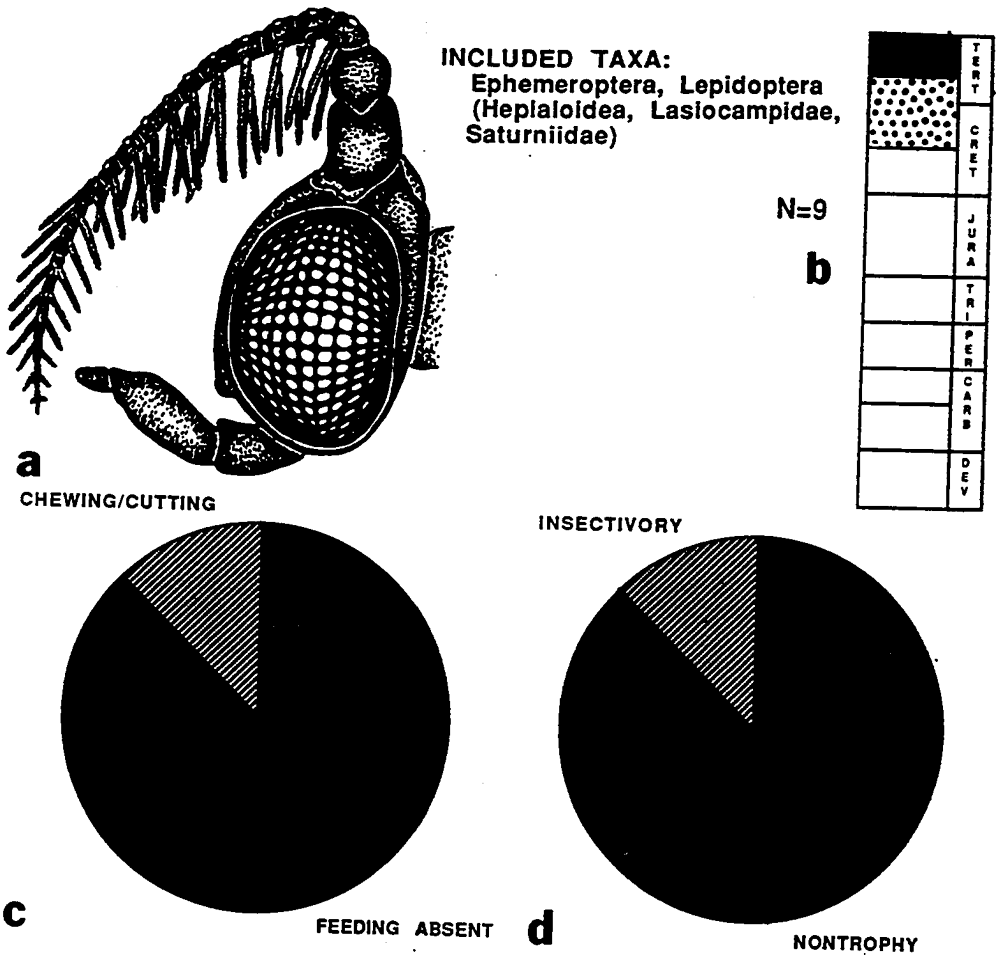


FIGURE 128. Overview of the Nontrophic Mouthpart Class. a, *Malacosoma neustria* Linneaus (Lepidoptera: Lasiocampidae, data-set no. 1199), after Rouchy (1964); b, taxonomic distribution, number of taxa examined and geochronologic range; c, functional-feeding-groups; d, dietary spectrum.

There are three types of mouthpart modification in nonsiphonate lepidopterans. Forms with vestigial galeae may lack a mouth and have an incomplete digestive tract and thus do not feed (Richards and Davies 1977, Faegri and van der Pijl 1980). Others have a functional mouth, digestive tract and anus, but use a flimsy, rudimentary "siphon" as an abbreviated sucking or possibly sponging organ (Willemstein 1987) for limited fluid-feeding. Still others are mandibulate forms that have lost most or all of a galeal siphon, but have retained mandibles that function in chewing food. Many accounts of the trophic habits of short-siphoned or rudimentary-siphoned lepidopterans are either equivocal, indicating only possible or facultative feeding on a particular host plant or plants, or they indicate no known plant hosts (Proctor and Yeo 1973, Faegri and van der Pijl 1980, Willemstein 1987).

Apparently all recent ephemeropterans do not feed and they house vestigial mouthparts that are generally expressed as unsclerified, structurally inconstant, flimsy appendages (Sternfeld 1907, Murphy 1922). Mouthpart degeneration commences during the late nymph stage and is concluded by the time of subimago emergence. There is no known record of feeding in any Recent adult ephemeropteran.

Structural Themes. Two structural themes within the Nontrophic Mouthpart Class are evident in Fig. 129. The first theme is Subcluster 1 (bracketed by data-set taxa 37 to 917 in Fig. 129) and consists of two adult ephemeropterans and anomalously an adult dolichopodid dipteran. Inclusion of a dipteran is based on the absence of several mouthpart elements, including mandibles, galeae, laciniae, glossae and

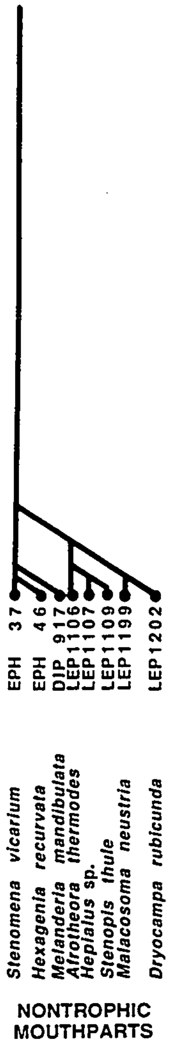


FIGURE 129. Cluster analysis dendrogram of taxa comprising the Nontrophic Mouthpart Class. See Fig. 28 for relationships of this mouthpart class to other mouthpart classes.

paraglossae. However the labial palps that are normally fused into a fleshy, sponging labellum in most adult dipterans are modified into functioning mandible-like structures (Aldrich 1922, Snodgrass 1922, Robinson and Vockeroth 1981) in which each labellar lobe is distally sclerotized into a hardened tooth that is movable at the base (Cregan 1941). This unusual condition for nominally labellate adult dipterans, has been scored as "mandibulate" for *Melanderia mandibulata* Aldrich, even though other character-states have placed it into the nontrophic class. Although formally included in the nontrophic class, *M. mandibulata* is a typical feeding adult dipteran and cannot be considered as nontrophic with nonfunctional mouthparts in the sense of an adult ephemeropteran or lepidopteran.

The second theme within the nontrophic cluster are adult hepialoid and bombycoid lepidopterans (Subcluster 2, taxa 1106 to 1202) that lack functioning mouthparts and possess mouthpart elements that assume the appearance of basally nonarticulating, poorly-sclerotized and structurally variable flaps. These taxa have nonsiphonate galeae that are often a pair of inconspicuous processes or less commonly recognizable lobate appendages. This phenomenon of siphonal reduction is probably quite common in all major groups of lepidopterans (see section on "Diversity and Natural History" above). Unlike the ephemeropterans of the Subcluster 1, lepidopterans of Subcluster 2 lack mandibles, laciniae, glossae and paraglossae.

Geochronologic History. The geochronologic history of the Nontrophic Mouthpart Class is generally poor, although it is better for ephemeropterans than for lepidopterans. For ephemeropterans, there is a grouping of fossil occurrences during the Permian, a hiatus during the Triassic and a second, larger grouping from the Jurassic to the Recent (Fig. 130). Adults of Permian clades of ephemeropterans--the Triplosobiodea and Protereismatoidea (Chernova 1980), perhaps subordinally distinct within the Ephemeroptera--bore functional, mandibulate mouthparts and were feeders as adults (Kukalová-Peck 1985). Evidence for this comes from well-preserved head and mouthpart structures from *Misthodotes zalesskyi* Chernova 1965 and *M. sharovi* Chernova 1965 of the family Misthototidae from Lower Permian deposits of the USSR [89] (Chernova 1965, 1970; Kukalová-Peck 1985) and from *Protereisma permianum* Sellards 1907 of the family Protereismatidae from the Lower Permian [90] of Kansas (Tillyard 1932). Although these Paleozoic ephemeropterans were ancestral to all Recent Ephemeroptera (Chernova 1980), they were considerably larger in body size than modern species and probably required food to remain viable as adults. As a result inferences regarding nontrophic ephemeropteran mouthparts based on Recent species extend to the Jurassic, during which all modern superfamilies and one extinct superfamily originated (Fig. 130). The overall Jurassic to Tertiary fossil record of the Ephemeroptera consists of nine superfamilies, ranging from the Siphlonuroidea which is abundantly represented to the Caenoidea which lacks fossil documentation. Other ephemeropteran superfamilies have fossil record documentation lying between these two extremes.

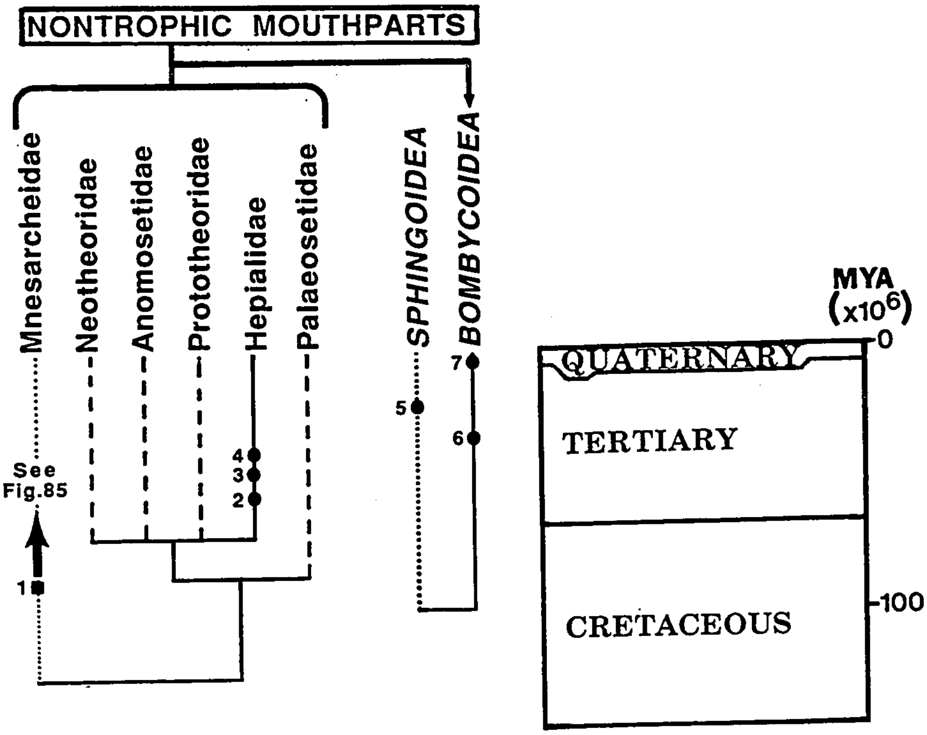


FIGURE 130. Geochronologic History of the Nontrophic Mouthpart Class. See Appendix F for taxa, localities and references corresponding to each fossil occurrence. The phylograms are after Kristensen (1978) for Hepialoidea and Scott (1986) and Kozlov (1988b) for Sphingoidea + Bombycoidea. (The Bombycoidea includes the families Saturniidae and Lasiocampidae.) The levels of analyses are the family for Hepialoidea and the superfamily for Sphingoidea + Bombycoidea. The outgroups are Mnesarchaeidae and Sphingoidea. For the geochronology of nontrophic members of the Ephemeroptera, see the cluster bracketed by the superfamilies Ephemeroidea to Caenoidea in Fig. 58. These fossil occurrences are not necessarily a complete inventory of all documented fossil members of this mouthpart class.

The geochronologic history of nontrophic lepidopterans is based largely on sister-group relationships of modern taxa, several Tertiary occurrences and a possible Late Cretaceous fossil occurrence. The only nontrophic families indicated by the data base are the Hepialidae, Lasiocampidae and Saturniidae, although many others are suspected (*vide supra*). The fossil record for these families is poor. Hepialids are recorded from the Lower Eocene of France as leaf-mines [27] (Piton 1940), from the Upper Eocene of New Zealand [21] (Harris 1984) and the Late Eocene/Early Oligocene of Great Britain [18] (Jarzembowski 1980); other hepialoid families lack fossil records. The sister-group to the Hepialoidea, the Mnesarchaeoidea (Kristensen 1984), may have a fossil occurrence in Late Cretaceous Siberian amber [37] (Skalski 1979b). Lasiocampids lack a fossil record whereas saturniids have two fossil occurrences--one from the Early Oligocene of Colorado [15] (Cockerell 1922) and the other from the Pleistocene of Finland (Koponen and Nukorteva 1973). Lasiocampids and saturniids are members of the superfamily Bombycoidea, whose probable sister-group, the Sphingoidea, has an earliest fossil occurrence from a caterpillar of the Early Miocene of Germany [7] (Zeuner 1931). These fossil data are coarse-grained and are only modestly useful in assessing the timing of origin of the Hepialidae, Lasiocampidae and Saturniidae. However they are consistent with suggestions by Kristensen (1978), Scott (1986) and Kozlov (1988) who indicate a Late Cretaceous origin for these groups.

Previous Designations. The apparent absence of feeding during the adult stage among several insect groups, especially ephemeropterans, lepidopterans, hymenopterans, dipterans and coleopterans has been recognized for some time (Brues 1972) and has been directly associated with mouthpart reduction. Denis and Bitsch (1973: 41) commented on four major modifications of insect mouthparts, one of which they termed "*réduction pièces buccales*" (Table 6). This theme was later discussed by Chaudonneret (1983) as a distinctive mouthpart class. Both Proctor and Yeo (1973) and Faegri and van der Pijl (1980) noted that members of many lineages that are active pollinivores and nectarivores of flowers also have members that do not feed. Thus the phenomenon of mouthpart reduction and associated aphagia has been documented, although generalizations have been on a lineage-by-lineage basis.

Reference to a **nontrophic** mouthpart class summarizes many of the above observations. As a discrete mouthpart class, nontrophics can be viewed as a solution for eliminating mouthpart structures that are unnecessary for short-lived adult phases whose sole function is reproduction. The term nontrophic has not been used in this sense previously.

Review of Literature. Documentation of nontrophic mouthparts has been provided principally for lepidopterans although Sternfeld (1907), Murphy (1922) and Needham, Traver and Hsu (1935) discussed and figured rudimentary mouthparts for species of the ephemeropterans *Chloeon*, *Ephemera*, *Hexagenia* and *Stenomena*. Mouthpart rudimentation in hepialoid lepidopterans has been documented by Mosher (1915), Philpott (1927) and Nielson and Scoble (1986). For saturniid lepidopterans Mosher (1915), Schmitt (1938), Snodgrass (1961) and Rouchy (1964) illustrated and discussed rudimentary mouthparts. A broader perspective that surveys the occurrence of spihonal loss and abbreviation in numerous families of lepidopterans can be found in Philpott (1927), Taylor (1957), Proctor and Yeo (1973) and Willemstein (1987).

8.11. Summary Statement

In this section I will summarize the two important consequences of mouthpart structure discussed in this chapter. These are (i) the associations between mouthpart class and functional-feeding-group and diet and (ii) the geochronologic history of hexapod mouthpart classes. Definitions of the mouthpart classes, their key features and other aspects are summarized under each mouthpart class discussion and are not reviewed here.

The direct associations that exist between mouthpart class, functional-feeding-group and diet have been provided in those figures providing an overview of each mouthpart class. These three categories represent the structural, functional and ecological dimensions of a single food-acquisition system. In the ensuing discussion, it is necessary to consider mouthpart classes as *structural* entities comprising physical elements, functional-feeding-groups as *functional* entities engaged in a process, and diet as an *ecologically*-based resource available for consumption. These three concepts are represented in the data-set of Appendix C and are explained in Appendix A. They represent qualitatively different kinds of data and thus must be considered individually. The structural basis of mouthpart classes was discussed in Section 5.2; note that the characters used are structural in nature but are chosen for their functional utility. The concept of a functional-feeding-group is a categorization of how mouthparts work; thus a single functional-feeding-group can occur in more than one mouthpart class, or a single mouthpart class may house several functional-feeding-groups. Although functional-feeding-groups are relatively well-constrained ecologically, they are also minimally documented in the mouthpart literature. For the purposes of this study the concept of a functional-feeding-group will not be pursued further because of insufficient documentation in the primary mouthpart literature and because one of the central goals of this study is to ascertain the associations between mouthpart structure and diet.

Dietary data is the least constrained of the three categories since it is dependent on generally anecdotal, sometimes unreliable field observations. For example, in some instances it is not clear whether the diet ascribed to a particular hexapod is documented by direct observational evidence, such as witnessing an insect feed on a particular substrate or examination of gut contents, or whether it is an indirect inference based on the association of an insect with a particular substrate in lieu of actual feeding, or based on laboratory feeding experiments that are not extrapolatable to the natural world. Because of these uncertainities, in the ensuing discussion I am considering the dietary repertoire of each mouthpart class as an average of all diets of individual taxa in the class. (For more detailed dietary data, see the appropriate figures in Sections 8.3 to 8.10.) These generalized diets may be conceived as feeding trajectories, some of which possess considerable variation and others that are highly stereotyped.

Some apterygotes, most paleopterans, orthopteroids, many adult holometabolans and some larval holometabolans bear mouthpart classes of the Mandibulate Series. These mouthpart classes are engaged in solid-food feeding and, to a lesser extent, particle-feeding. Within solid-food feeding, the spectrum of diets consumed by each of the 13 mouthpart classes is immense. Whereas members of the entognathate, monocondylate and mortar-and-pestle mouthpart classes are largely detritivores or necrovores in litter, soil or under bark; raptorial-ectognathates are obligate predatory insectivores in the air; rostrates are opportunistic insect necrovores; and rhynchophorates consume indurated substrates such as seeds, grain and wood. The pectinate, mouthbrush and mandibulobrustiate mouthpart classes are dominantly aquatic filter-feeders, sieve-strainers or herbivores. In distinct contrast, adult-ectognathates, larval-ectognathates and maxillolabiates each have very broad, uncharacterizible diets that collectively include all major diet categories. Sericterates have focused principally on herbivory by either external foliage feeding, leaf-mining or leaf-galling, or are necrovorous or insectivorous for those forms who receive provisioned food.

Larvae of three holometabolous orders--Planipennia, Coleoptera and Diptera--have independently acquired suctorial tubulate mandibles or mandible/maxilla complexes. This fluid-feeding group consists of members of the fossate-complex, tubulomandibulate and mouthhook mouthpart classes is very strongly tied to carnivory (principally insectivory) and to a lesser extent necrovory and herbivory.

Hemipteroids and adults of most holometabolous groups are fluid feeders that are associated with either the stylate-haustellate series, which sequesters integument-bound biological fluid, or the labellate, siphonate and glossate series, which imbibe exposed fluids. Among the former group, plant sap and vertebrate blood are the two principal food sources. Nine mouthpart classes exploit membrane-bound fluids by using combinations of long, ensheathed stylets that either pierce or saw in conjunction with various sucking pumps. The dietary repertoire of these fluid feeders is eclectic and includes not only plant sap and blood but also nectar, fungi, pollen and carrion. Of these nine mouthpart classes, five are either entirely or highly dominated by ectoparasitic sanguinivores on mammals. (Fig. 131 depicts the percentage distribution of the 34 extant mouthpart classes.)

For mouthpart classes of the labellate, siphonate and glossate series, which overwhelmingly exploit fluids exposed on surfaces, there has been a predominant association with seed plants. Materials consumed from seed plants include exposed fluids such as sap, nectar and particulate matter such as spores and pollen. Insect groups participating in feeding on exposed surface fluids include a few adult coleopteran groups, nannochoristid mecopterans, trichopterans, most adult dipterans, lepidopterans, and vespoid, sphecoid and apoid hymenopterans. Many adult holometabolous insects have converged on highly stereotyped mouthpart structures within the labellate, siphonate and glossate series.

Exemplifying the highest degree of structural convergence within a mouthpart class has been the independent origin of several coleopteran ectognathous-stylate groups that are collectively represented by small, cryptic forms that feed principally on fungi. This dietary trend is paralleled by two lineages of entognathous-stylate groups, which are

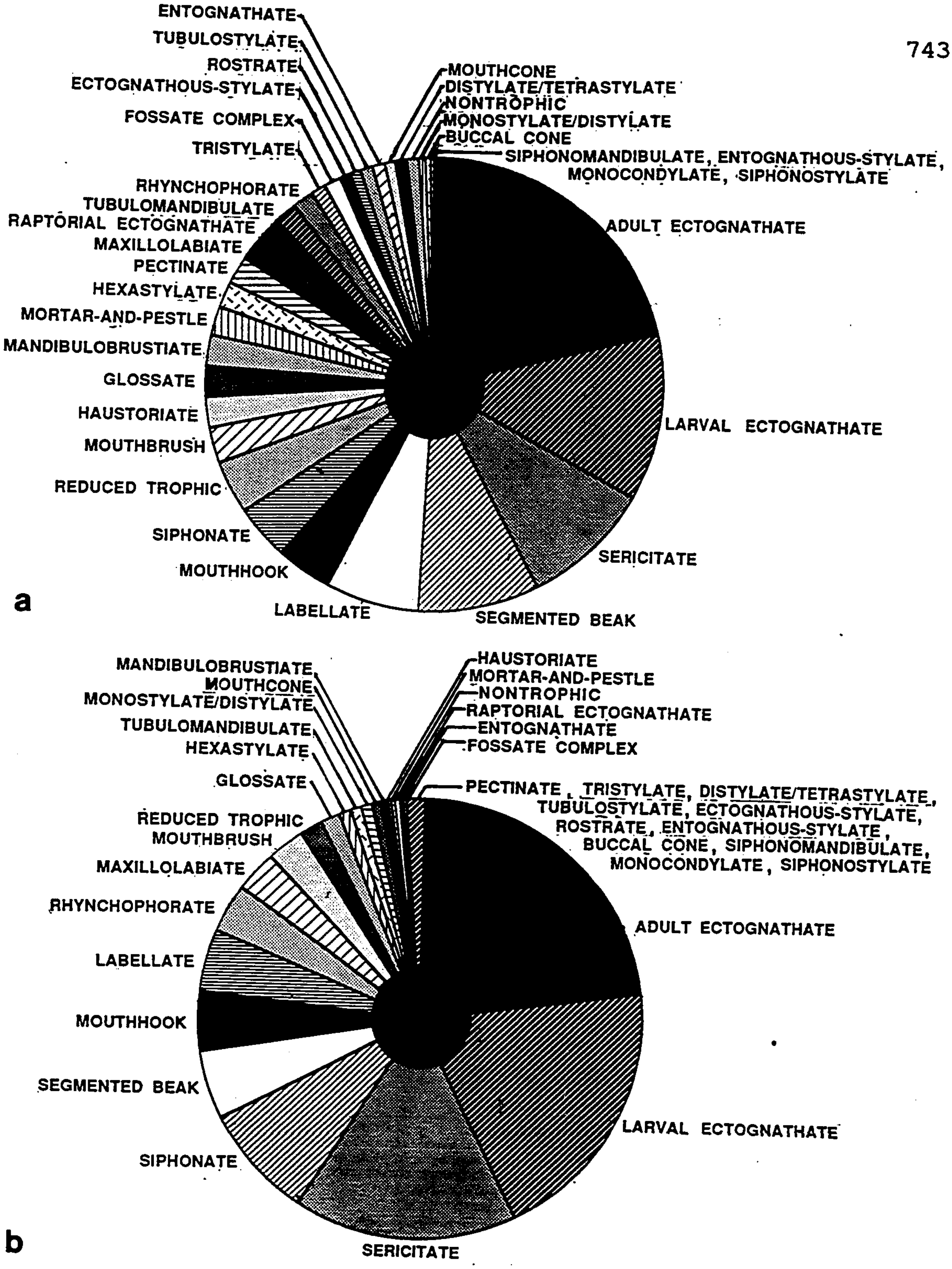


FIGURE 131. Percentage distribution of mouthpart classesin the Recent hexapod fauna. Every taxon in the data set is treated equally; thus conspecific larval and adult stages belonging to different mouthpart classes are included. Thus these graphs represent mouthpart diversity and not taxonomic diversity. a, Mouthpart diversity from the data set in this study. b, Mouthpart diversity extrapolated to the global insect fauna, using diversity abundance values in Appendix D.

dominantly small, cryptic fungivores. (Table 8 lists examples of these and other taxa whose mouthparts are atypical for their respective taxonomic group, and this indicates the pervasiveness of structural convergence.)

Lastly many groups of hexapods have experienced mouthpart reduction that represents either aphagy in the adult stage (Ephemeroptera, Lepidoptera) or endoparasitism in the larval stage (Strepsiptera, Hymenoptera). Mouthpart reduction transformations apparently occurred randomly among insects and lack any major taxonomic preferences.

The geochronological pattern of appearance of mouthpart classes is characterized by a five-phase pattern. (For the following discussion, Figs. 132 to 134 provide geochronologic ranges for each mouthpart class.) First, the earliest known hexapods housed entognathate, entognathous-stylate and monocondylate mouthparts during the Lower Devonian. While the fossil record of hexapods is virtually nonexistent from the Middle Devonian to Lower Carboniferous, by earliest Late Carboniferous time several additional, mostly mandibulate, mouthpart classes appeared. This second phase was a varied suite of polyneopterans that possessed adult-ectognathate, larval-ectognathate, raptorial-ectognathate, pectinate and probably mandibulobrustiate mouthparts. Some of these mandibulate mouthpart classes are associated with filter-feeding (pectinates and mandibulobrustiates) and have their earliest occurrences during the Late Carboniferous whereas wereas others were solid-food consumers of plant and animal materials. (An extinct stylate-haustellate mouthpart class that was not analyzed in this study was also present; other nonsurviving mouthpart classes undoubtedly were

TABLE 8

DATASET TAXA WHOSE MOUTHPART CLASS ASSIGNMENTS ARE UNUSUAL FOR THEIR RESPECTIVE TAXONOMIC GROUP

Order	Mouthpart Class Assignment of Stereotyped Groundplan*	Exceptions to Stereotyped Groundplan of Mouthpart Class*	Data-Set No.	Mouthpart Class Assignment for the Exception	References*
Collembola	Entognathate	*Neanura muscorum* (Neanuridae)	(10)	Entognathous-Stylate	Schaller & Wolter 1963; Wolter 1963
Orthoptera	Adult-Ectognathate	*Cooloola propator* (Cooloolidae)	(98)	Ectognathous-Stylate	Rentz 1980,1987 Stylate
Mallophaga	Mortar-and-Pestle	*Haematomyzus elephantis* (Haematomyzidae)	(214)	Buccal Cone	Snodgrass 1944,1947; Mukerji & Sen-Sarma 1955
Neuroptera	Adult-Ectognathate	*Nemoptera sinuata* (Nemopteridae)	(388)	Rostrate	Crampton1921c,1923b; Withycombe 1923
Neuroptera	Adult-Ectognathate	*Nemopterella* sp. (Nemopteridae)	(389)	Rostrate	Acker 1958
Neuroptera	Adult-Ectognathate	*Palmipenna aeoloptera* (Nemopteridae)	(390)	Glossate	Picker 1987
Coleoptera	Adult-Ectognathate	*Sphaerius politus* (Sphaeriidae)	(401)	Ectognathous-Stylate	Stickney 1923; Crowson 1981
Coleoptera	Adult-Ectognathate	*Clinidium mexicanum* (Rhysodidae)	(403)	Ectognathous-Stylate	Pauly 1915
Coleoptera	Adult-Ectognathate	*Omoglymmus americanus* (Rhysodidae)	(404)	Ectognathous-Stylate	Pauly 1915; Stickney 1923
Coleoptera	Larval-Ectognathate	*Brychius**sp. (Haliplidae)	(429)	Tubulo-mandibulate	Jaboulet 1960
Coleoptera	Larval-Ectognathate	*Haliplus** sp. (Haliplidae)	(430)	Tubulo-mandibulate	Peterson 1951; Jaboulet 1960
Coleoptera	Larval-Ectognathate	*Peltodytes** sp. (Haliplidae)	(432)	Tubulo-mandibulate	Peterson 1951; Jaboulet 1960
Coleoptera	Larval-Ectognathate	*Pelobia tardus** (Hygrobiidae)	(434)	Tubulo-mandibulate	Pauly 1915; Balfour-Browne 1922
Coleoptera	Larval-Ectognathate	*Cybister fimbriolatus** (Dytiscidae)	(437)	Tubulo-mandibulate	Peterson 1951; [De-Marzo 1977a, 1979]
Coleoptera	Larval-Ectognathate	*Dytiscus** sp. (Dytiscidae)	(439)	Tubulo-mandibulate	Korschelt 1924; Anderson 1936

TABLE 8 (Continued)

Order	Mouthpart Class Assignment of Stereotyped Groundplan*	Exceptions to Stereotyped Groundplan of Mouthpart Class*	Data Set No.	Mouthpart Class Assignment for the Exception	References*
Coleoptera	**Larval-Ectognathate**	*Hyphydrus aubei** (Dytiscidae)	(440)	**Tubulo-mandibulate**	DeMarzo 1977b
Coleoptera	**Larval-Ectognathate**	*Laccophilus testaceus** (Dytiscidae)	(441)	**Tubulo-mandibulate**	Demarzo 1976b, 1978
Coleoptera	**Larval-Ectognathate**	*Oreodytes rivalis** (Dytiscidae)	(442)	**Tubulo-mandibulate**	DeMarzo 1976b, 1978
Coleoptera	**Larval-Ectognathate**	*Dineutes** sp. (Gyrinidae)	(444)	**Tubulo-mandibulate**	Anderson 1936; Peterson 1951
Coleoptera	**Larval-Ectognathae**	*Orechtochilus villosus** (Gyrinidae)	(446)	**Tubulo-mandibulate**	Noars 1956; Bitsch 1966
Coleoptera	**Adult-Ectognathate**	*Aculomicrus pusio* (Hydrophilidae)	(480)	**Siphono-mandibulate**	Smetana 1975
Coleoptera	**Larval-Ectognathate**	*Berosus** sp. (Hydrophilidae)	(481)	**Maxillolabiate**	Smetana 1975
Coleoptera	**Adult-Ectognathate**	*Jentozkus plaumanni* (Eucinetidae)	(498)	**Ectognathous Stylate**	Vit 1977
Coleoptera	**Adult-Ectognathate**	*Tohklezkus ponticus* (Eucinetidae)	(499)	**Ectognathous Stylate**	Vit 1977, 1981
Coleoptera	**Larval-Ectognathate**	*Chalcophora virginiensis** (Buprestidae)	(535)	**Mouthbrush**	Boving & Craighead 1931; Peterson 1951
Coleoptera	**Larval-Ectognathate**	*Chrysobothris femorata** (Buprestidae)	(536)	**Mouthbrush**	Boving & Craighead 1931; Peterson 1951
Coleoptera	**Larval-Ectognathate**	*Melasis rufipennis** (Eucnemidae)	(559)	**Reduced-Trophic**	Boving & Craighead 1931; [Peterson 1951]
Coleoptera	**Larval-Ectognathate**	*Brachyspectra fulva** (Brachyspectridae)	(561)	**Tubulo-mandibulate**	Boving & Craighead 1931
Coleoptera	**Larval-Ectognathte**	*Calochromis tarsalis** (Lycidae)	(562)	**Tubulo-mandibulate**	Gardner 1946; Crowson 1981
Coleoptera	Larval-Ectognathate	Calopteron reticulatum* (Lycidae)	(563)	Tubulo-mandibulate	Boving & Craighead 1931; [Peterson 1951]
Coleoptera	**Larval-Ectognathate**	*Eros aurora** (Lycidae)	(564)	**Tubulo-mandibulate**	Verhoeff 1923;[Boving & Craighead 1931]

TABLE 8 (Continued)

Order	Mouthpart Class Assignment of Stereotyped Groundplan*	Exceptions to Stereotyped Groundplan of Mouthpart Class*	Data Set No.	Mouthpart Class Assignment for the Exception	References*
Coleoptera	Larval-Ectognathate	*Drilius concolor** (Drilidae)	(566)	Tubulo-mandibulate	Boving & Craighead 1931
Coleoptera	Larval-Ectognathate	*Phenogodes laticollis** (Phenogodidae)	(567)	Tubulo-mandibulate	Boving & Craighead 1931; Peterson 1951
Coleoptera	Larval-Ectognathate	*Lampyris noctiluca** (Lampyridae)	(569)	Tubulo-mandibulate	Vogel 1915; Boving & Craighead 1931
Coleoptera	Larval-Ectognathate	*Lamprophorus tenebrosus** (Lampyridae)	(570)	Tubulo-mandibulate	Raj 1943; Gardner 1946
Coleoptera	Larval-Ectognathate	*Luciola dubia** (Lampyridae)	(571)	Tubulo-mandibulate	Gardner 1946; [Arnett 1963]
Coleoptera	Larval-Ectognathate	*Photinus pyralis** (Lampyridae)	(572)	Tubulo-mandibulate	Boving & Craignead 1931; [Peterson 1951]
Coleoptera	Larval-Ectognathate	*Photurus pennsylvanica** (Lampyridae)	(573)	Tubulo-mandibulate	Boving & Craighead 1931; Peterson 1951
Coleoptera	Larval-Ectognathate	*Cantharis rustica** (Cantharidae)	(575)	Tubulo-mandibulate	Boving & Craighead 1931; Peterson 1951
Coleoptera	Adult-Ectognathate	*Aculagnathus mirabilis* (Cerylonidae)	(624)	Ectognathous-Stylate	Besuchet 1973; Sen Gupta & Crowson 1973
Coleoptera	Adult-Ectognathate	*Axiocerylon cavicolle* (Cerylonidae)	(625)	Ectognathous-Stylate	Sen Gupta & Crowson 1973
Coleoptera	Adult-Ectognathate	*Cautomus sugerens* (Cerylonidae)	(626)	Ectognathous-Stylate	Besuchet 1972; Dajoz 1976
Coleoptera	Adult-Ectognathate	*Cerylcautomus floridensis* (Cerylonidae)	(627)	Ectognathous-Stylate	Sen Gupta & Crowson 1973
Coleoptera	Adult-Ectognathate	*Lapecautomus dybasi* (Cerylonidae)	(629)	Ectognathous-Stylate	Sen Gupta & Crowson 1973
Coleoptera	Adult-Ectognathate	*Philothermus bicavis* (Cerylonidae)	(631)	Ectognathous-Stylate	Sen Gupta & Crowson 1973; [Dajoz 1976]
Coleoptera	Adult-Ectognathate	*Hoplicnema sallaei* (Corylophidae)	(633)	Ectognathous-Stylate	Pakaluk 1987
Coleoptera	Adult-Ectognathate	*Macrosiagon ferrungineum* (Rhipiphoridae)	(653)	Siphonate	[Rivnay 1929]; Grandi 1926, 1937, 1960

TABLE 8 (Continued)

Order	*Mouthpart Class Assignment of Stereotyped Groundplan**	*Exceptions to Stereotyped Groundplan of Mouthpart Class**	*Data Set No.*	*Mouthpart Class Assignment for the Exception*	*References**
Coleoptera	**Larval-Ectognathate**	*Macrosiagon ferrungineum** (Rhipiphoridae)	(654)	**Reduced-Trophic**	Grandi 1926,1937, 1959
Coleoptera	**Adult-Ectognathate**	*Rhipiphorus dimidiatus* (Rhipiphoridae)	(655)	**Siphono-mandibulate**	Crampton1923a, 1923b; Stickney 1923
Coleoptera	**Larval-Ectognathate**	*Rhizostylops inquirendus** (Rhipiphoridae)	(656)	**Reduced-Trophic**	Silvestri 1905
Coleoptera	**Adult-Ectognathate**	*Leptopalpus rostratus* (Meloidae)	(677)	**Siphono-mandibulate**	Handschin 1929; Jeanell 1960; Grinfel'd 1975
Coleoptera	**Adult-Ectognathate**	*Nemognatha piezata* (Meloidae)	(679)	**Siphono-mandibulate**	Crampton 1923b; Williams 1938
Mecoptera	**Rostrate**	*Nannochorista dipteroides* (Nannochoristidae)	(760)	**Labellate**	Crampton 1921a, b, 1942; Tillyard 1935
Diptera	**Mouthhook**	*Synneuron decipiens** (Hyperoscelidae)	(858)	**Reduced-Trophic**	Mamaev & Krivosheina 1969; [Teskey 1976]
Diptera	**?Hexastylate**	*Nymphomyia alba* (Nymphomyiidae)	(873)	**Reduced-Trophic**	Tokunaga 1932, 1935
Diptera	**Monostylate/ Distylate**	*Ogcodes costatus* (Acroceridae)	(897)	**Reduced-Trophic**	Peterson 1916; [Crampton 1942]
Diptera	**?Monostylate/ Distylate**	*Melanderia mandibulata* (Dolichopodidae)	(917)	**Nontrophic**	Aldrich 1922; Cregan 1941; Snodgrass 1922a
Diptera	**Labellate**	*Gasterophilus intestinalis* (Gasterophilidae)	(988)	**Reduced-Trophic**	Peterson 1916; Cole 1969
Trichoptera	**Mandibulo-brustiate**	*Phryganopsyche latipennis** (Phryganopsychidae)	(1051)	**Larval-Ectognathate**	Wiggins 1959
Lepidoptera	**Siphonate**	*Heterobathmia pseudo*-crania (Heterobathmiidae)	(1088)	**Adult-Ectognathate**	Kristensen & Nielsen 1979
Lepidoptera	**Siphonate**	*Micropteryx calthella* (Micropterygidae)	(1090)	**Adult-Ectognathate**	[Busck & Boving 1914]; 1979
Lepidoptera	**Siphonate**	*Mnemonica auricyanea* (Micropterygidae)	(1092)	**Adult-Ectognathate**	Busck & Boving 1914; Crampton 1920b
Lepidoptera	**Siphonate**	*Palaeomicroides fasciatella* (Micropterygidae)	(1093)	**Adult-Ectognathate**	Issiki 1931

TABLE 8 (Continued)

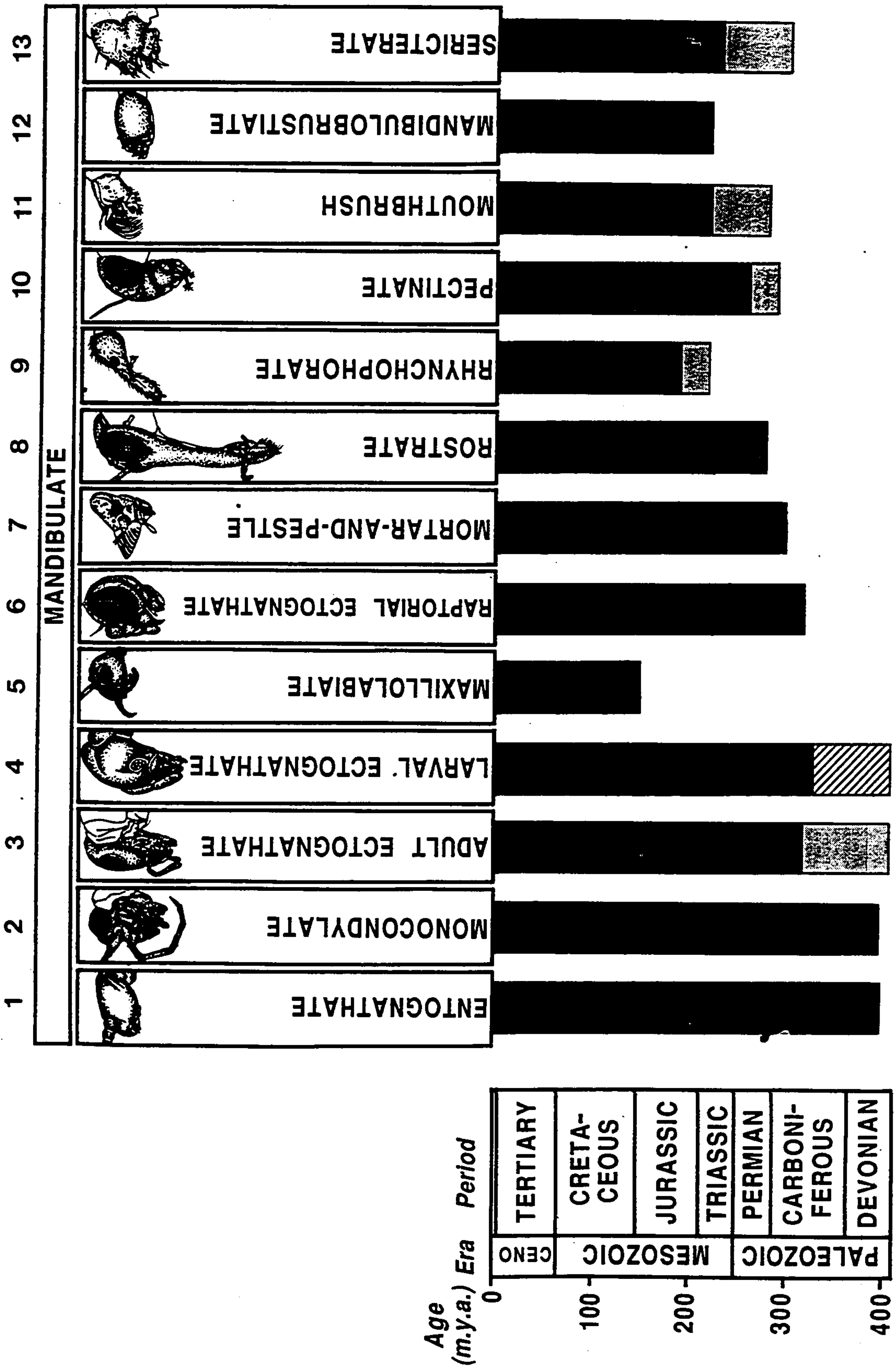
Order	Mouthpart Class Assignment of Stereotyped Groundplan	Exceptions to Stereotyped Groundplan of Mouthpart Class*	Data-Set No.	Mouthpart Class Assignment for the Exception	Referemces*
Lepidoptera	**Siphonate**	*Sabatinca auruncella* (Micropterygidae)	(1094)	**Adult-Ectognathate**	Genthe 1898; Tillyard 1923; [Issiki 1931]
Lepidoptera	**Siphonate**	*Agathiphaga vitiensis* (Agathiphagidae)	(1096)	**Adult-Ectognathate**	Dumbleton 1952; Kristensen 1984b
Lepidoptera	**Siphonate**	*Afrotheora thermodes* (Hepialidae	(1106)	**Nontrophic**	Nielsen & Scroble 1896.
Lepidoptera	**Siphonate**	*Hepialus* sp. (Hepialidae)	(1107)	**Nontrophic**	Kellogg 1895; Philpott 1927
Lepidoptera	**Siphonate** (Hepialidae)	*Stenopis thule*	(1109)	**Nontrophic**	Mosher 1915
Lepidoptera	**Siphonate**	*Phyllocnistis suffusella* (Phyllocnistidae)	(1123)	**Mouthbrush**	Jayewickreme 1940; Grandi 1949
Lepidoptera	**Siphonate**	*Gracillaria stigmatella** (Gracillariidae)	(1124)	**Mouthbrush**	[DeGryse 1915]; Grandi 1959; [MacKay 1972]
Lepidoptera	**Siphonate**	*Somatobrachys infuscata* (Somabrachyidae)	(1156)	**Reduced-Trophic**	Jordan 1916
Lepidoptera	**Siphonate**	*Epipomponia elongata* (Epipyropidae)	(1158)	**Reduced-Trophic**	Jordan 1928
Lepidoptera	**Siphonate**	*Malacosoma neustria* (Lasiocampidae)	(1199)	**Nontrophic**	[Schmitt 1938]; Rouchy 1964
Lepidoptera	**Siphonate**	*Dryocampa rubicunda* (Saturniidae)	(1202)	**Nontrophic**	Mosher 1915
Lepidoptera	**Siphonate**	*Calyptra eustrigata* (Noctuidae)	(1219)	**Siphonostylate**	Banziger 1970, 1971; Smith 1985
Lepidoptera	**Siphonate**	*Othreis materna* (Noctuidae)	(1223)	**Siphonostylate**	[Darwin 1875]; Srivastava & Bogawat 1969
Hymenoptera	**Maxillolabiate**	*Ceratosolen aculeatus* (Torymidae)	(1281)	**Glossate**	Grandi [1935], 1939
Hymenoptera	**Maxillolabiate**	*Fedschenkia grossa* (Sapygidae)	(1306)	**Glossate**	DeSaussure 1880; Brothers 1975

TABLE 8 (Continued)

Notes

*Stereotyped mouthpart class assignments of larger taxonomic groupings to which the exceptions belong are determined by presence of a dominant mouthpart class as a theme, and is evaluated mostly at the ordinal level and less commonly at the subordinal to familial level. Taxa with asterisks are subadult forms. The reference citation format follows that of Appendix B: unbrackeded references apply to the species indicated and bracketed references apply to congeneric species. See Appendix B for additional documentation.

FIGURE 132. Geochronologic distribution of mouthpart classes of the Mandibulate Series. The solid pattern indicates direct evidence from fossil occurrences, including larvae of taxa from adult-stage mouthpart classes, and vice-versa. The dotted pattern indicates indirect evidence for the inferred presence of a mouthpart class by the occurrence of relevant, fossil sister-group taxa. The slashed pattern indicates more remote indirect evidence such as trace-fossils and fossil forms whose constituent higher taxa were not analyzed in this study. The geochronologic scale is from Harland et al. (1982).


MANDIBULATE
1
ENTOGNATHATE
2
MONOCONDYLATE
3
ADULT ECTOGNATHATE
4
LARVAL. ECTOGNATHATE
5
MAXILLOLABIATE
6
RAPTORIAL ECTOGNATHATE
7
MORTAR-AND-PESTLE
8
ROSTRATE
9
RHYNCHOPHORATE
10
PECTINATE
11
MOUTHBRUSH
12
MANDIBULOBRUSTIATE
13
SERICTERATE
Period
TERTIARY
CRETA-CEOUS
JURASSIC
TRIASSIC
PERMIAN
CARBONI-FEROUS
DEVONIAN
Era
CENO
MESOZOIC
PALEOZOIC
Age (m.y.a.)
0
100
200
300
400

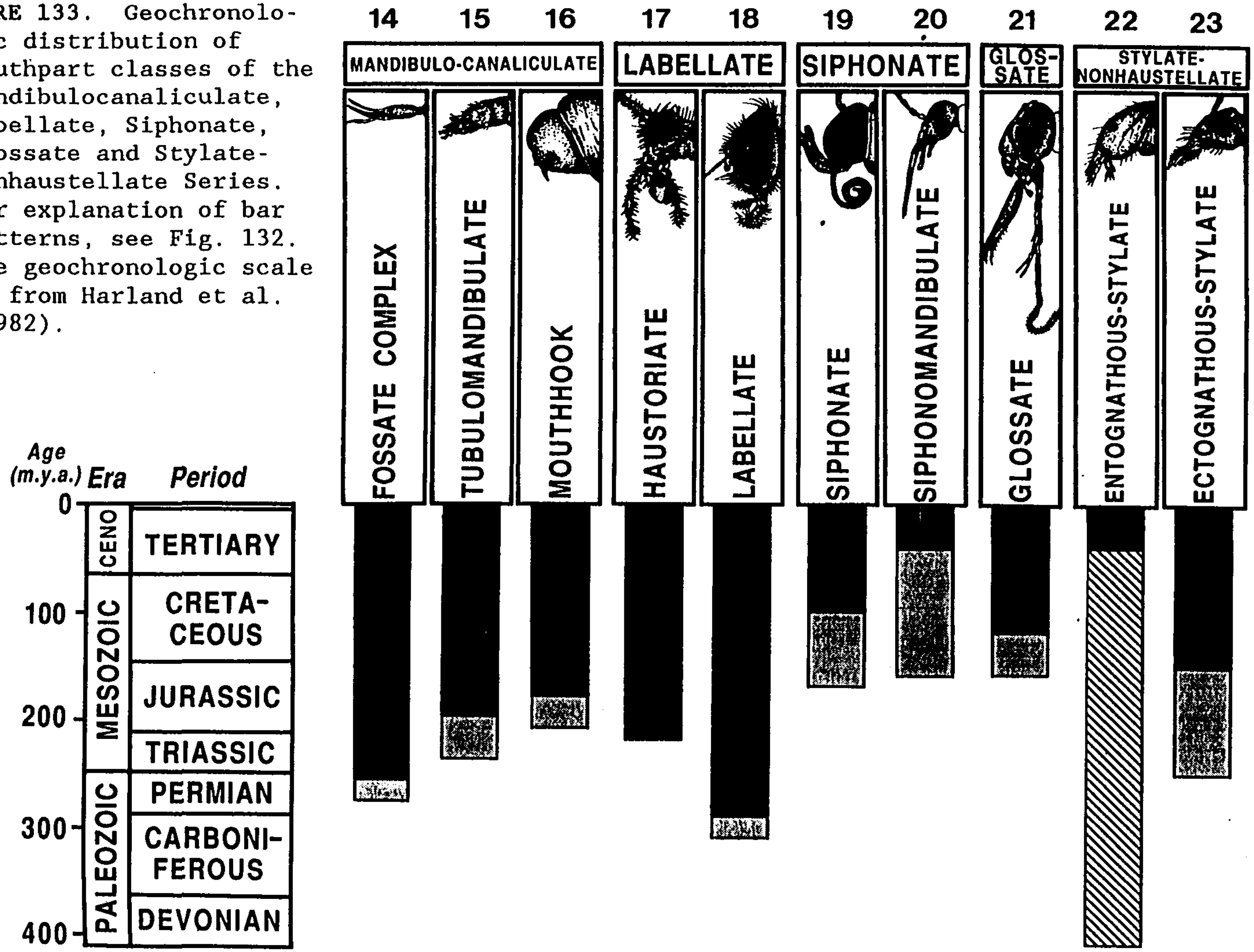


FIGURE 133. Geochronologic distribution of mouthpart classes of the Mandibulocanaliculate, Labellate, Siphonate, Glossate and Stylate-Nonhaustellate Series. For explanation of bar patterns, see Fig. 132. The geochronologic scale is from Harland et al. (1982).

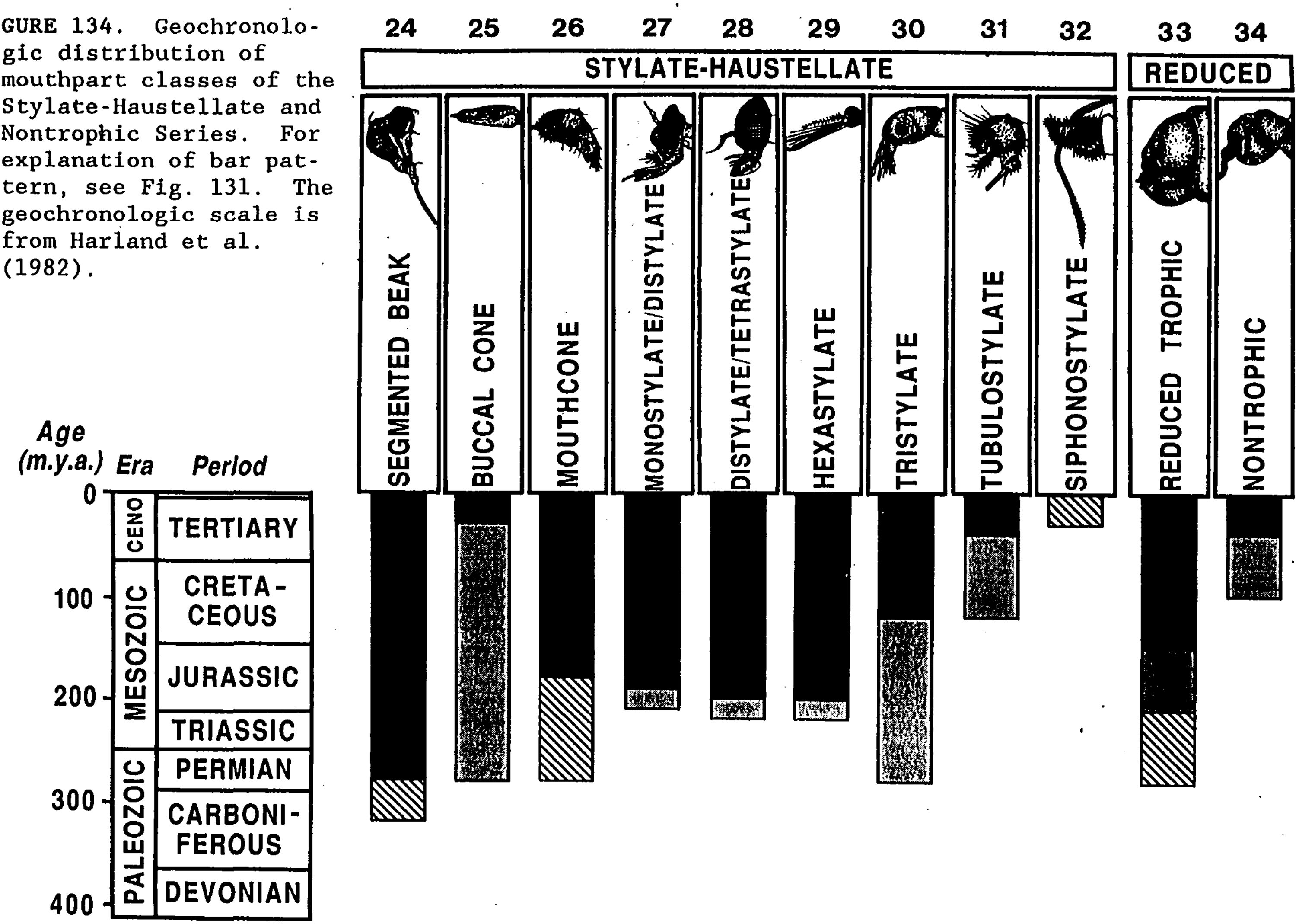


FIGURE 134. Geochronologic distribution of mouthpart classes of the Stylate-Haustellate and Nontrophic Series. For explanation of bar pattern, see Fig. 131. The geochronologic scale is from Harland et al. (1982).

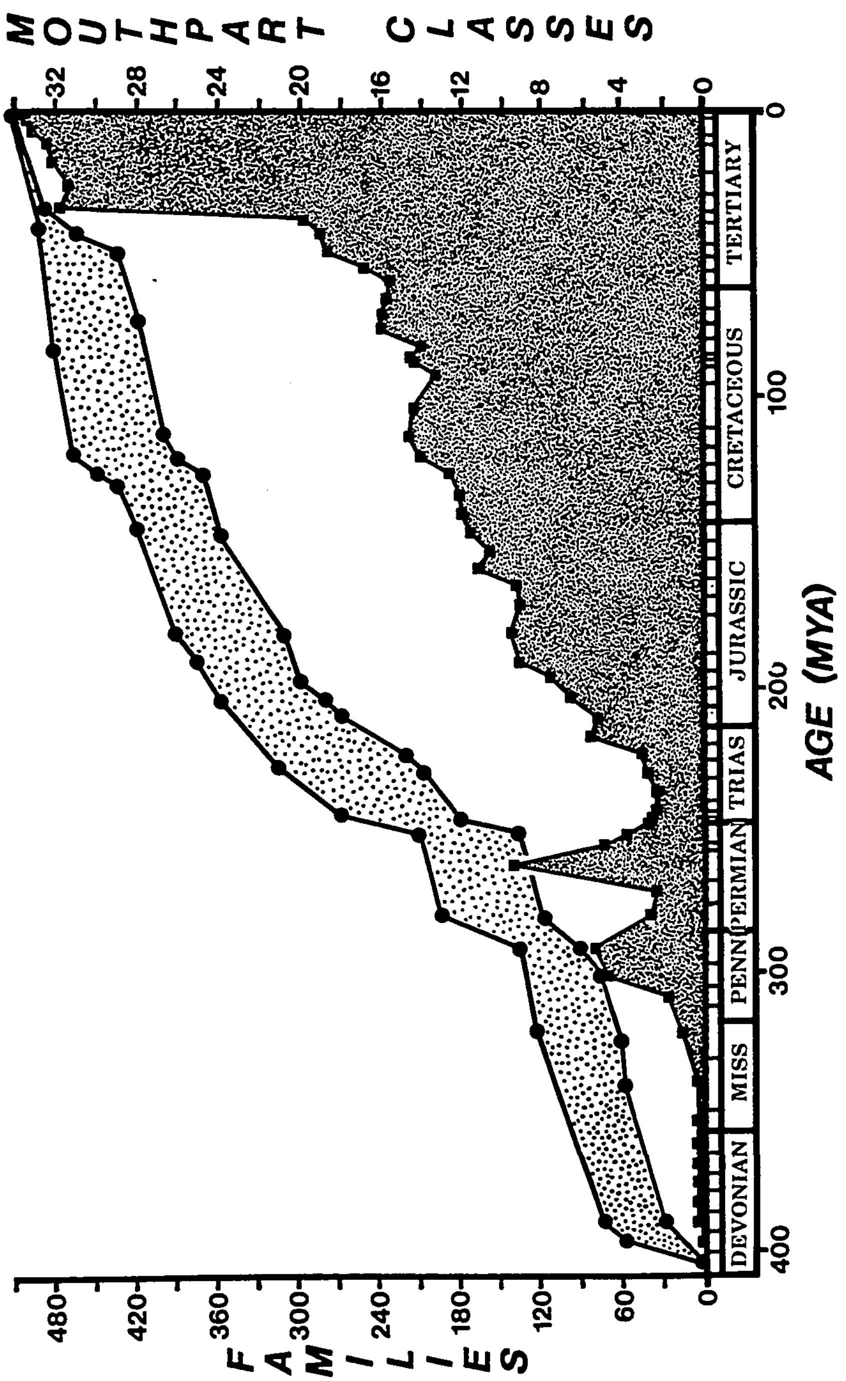
present.) After the probable origin of hemipteroids and holometabolans during the Late Carboniferous the third phase commenced during the Early Permian, when there was a proliferation of new mouthpart classes. These groups evolved predominantly plant-feeding mortar-and-pestle, mouthcone and segmented-beak mouthparts among hemipteroids and rostrate, haustoriate, fossate-complex, sericterate and nontrophic mouthpart classes among holometabolans. Nontrophic mouthparts were a consequence of the larva becoming the exclusive feeding stage in several holometabolous groups.

During the Late Triassic to Early Jurassic, several stylate-haustellate groups had evolved, corresponding to the fourth phase of mouthpart evolution. This phase is associated with an adaptive radiation of dipterans and siphonapterans that bore stylate-haustellate monostylate/distylate, distylate/tetrastylate, hexastylate and tristylate mouthparts that exploited tissue-bound fluids, as well as sponging labellate mouthparts. The taxonomically associated larval groups associated with this radiation bore filter-feeding mouthbrush and fluid-feeding mouthhook mouthparts. The fifth major phase in hexapod mouthpart innovation occurred during the Late Jurassic to Early Cretaceous, when groups closely associated with seed (but not necessarily angiospermous) plants appeared, including the durophagous rhynchophorate and the exposed fluid-feeding siphonate and glossate mouthpart classes. The penecontemporaneous origin of ectognathous-stylate mouthparts occurred among several groups of small fungivorous coleopterans; maxillolabiate mouthparts appeared in several groups of wasp and antlike apocritan hymenopterans. Groups represented by a relatively nondiverse membership or by forms with poor fossilization potential include the nectarivorous and sanguinivorous siphonomandibulate and the sanguinivorous, buccal-cone, tubulostylate and siphonostylate mouthpart classes that are ectoparasitic on tetrapods. Based on the mammalian hosts of these latter three classes, it is conceivable that they originated during the early Tertiary. However their sister-groups occur during the Mesozoic and even Late Paleozoic, and available warm- and cold-blooded tetrapod hosts were available during this interval.

From this brief historical sketch, the following broad geochronological pattern of the appearance of mouthpart structure is derived. The earliest and most primitive hexapod mouthparts are entognathous and are represented by both mandibulate and relatively advanced stylate-honhaustellate forms; adult-ectognathates are probably as old. All these classes are represented by primitively flightless insects. Among pterygote insects variations of the mandibulate condition appeared in both immature (nymphal) and adult forms, with pronounced differentiation occurring between immature and adult life-stages in odonatans and ephemeropterans. The subsequent appearance of holometaboly exerted a profound influence on mouthpart development of immature and adult forms, with larval stages acquiring qualitatively different modifications of mandibles and maxillae for active predation (fossate-complex, tubulomandibulates, mouthhooks), becoming filter-feeders (mouthbrushes, mandibulobrustriates), or modifying the general ectognathous condition to specialize on external herbivory or leaf-mining (sericterates). The adults of holometabolans predominantly became fluid feeders, accomplishing this transition as two major trends: feeding on biologically encapsulated food (stylate-haustellates) or feeding on exposed fluids produced mostly by plants (labellates, siphonates, glossates). In the modern flora, these fluids often consist of angiosperm nectar and pollen that can be imbibed as a suspension. However, some of these middle Mesozoic mouthparts, especially labellates, antedate angiospermy and indicate associations with preangiospermous seed plants. (Alternatively, but less likely, an earlier origin for angiosperms has been argued on cladistic grounds [Doyle and Donoghue 1987].) Besides labellates, the same relationship exists for rhynchophorates, which first appear during the Late Jurassic. Both trends involved profound changes in mouthpart structure and pronounced stereotypy of newly consolidated mouthpart elements, for example the dipteran stylate proboscis or labellum, the lepidopteran siphon and the glossate tongue. Within both trends, mouthparts designed for fluid-feeding became secondarily modified for sucking epidermal or subepidermal fluids by various animal ectoparasites.

One result of the foregoing pattern is that mouthpart class evolution is largely decoupled from family-level taxonomic evolution (Fig. 135). When the rate of family-level taxonomic diversification of hexapods is compared to the rate of structural diversification of hexapod mouthpart classes, there is a considerable separation between these two trends during the Early and Middle Mesozoic. Consequently, while taxonomic diversity did not dramatically increase until the Cretaceous and Early Tertiary, 91% of all mouthpart types were in existence by the Middle Jurassic. Several factors mitigate against taphonomic artifacts accounting for this relationship: (i) the data base for the taxonomic and mouthpart data-sets is coincident, (ii) the fossil

FIGURE 135. A comparison of familial diversity versus mouthpart class diversity for hexapods during the Phanerozoic. The diversity curve is derived from Sepkoski and Hulver (1985), with modifications (mostly additions) by myself. The mouthpart classes represent only the modern insect fauna of this study. The upper mouthpart abundance curve represents inferred presence based on sister-group relationships; the lower abundance curve indicates direct evidence from corroborated fossil occurrences only. It is suggested that the upper curve is a more realistic measure of true mouthpart diversity during the past. Note the disparity between the rate of mouthpart origination of the modern insect fauna and the rate of origination of hexapod families. Inclusion of extinct mouthpart classes of the Paleozoic would augment this disparity.


FAMILIES
480
420
360
300
240
180
120
60
0
MOUTHPART CLASSES
32
28
24
20
16
12
8
4
0
DEVONIAN
MISS
PENN
PERMIAN
TRIAS
JURASSIC
CRETACEOUS
TERTIARY
400
300
200
100
0
AGE (MYA)

insect record is better for the Jurassic than the Cretaceous, suggesting a bias favoring greater taxonomic representation during the Jurassic and (iii) if extinct Late Paleozoic mouthpart classes were included in the mouthpart data-set, the disparity would be even greater. This macroevolutionary pattern provides strong corroboration for the ecological saturation hypothesis, wherein within an ecosystem, ecological roles (such as mouthpart classes) attain an early maximum and remain numerically stable thereafter. It does not support the expanding resources hypothesis, which posits an increasing number of fundamental ecological roles during the evolutionary history of an ecosystem.

CHAPTER 9

LIMITATIONS OF THE DATA AND RESULTS

In a study of this size, it is important to evaluate all sources of error, both at the data-collection and at the data-analysis levels. In this section the major potential sources of error are addressed. They include the reliability of the source literature from which the morphological and structural data were retrieved, choice and appropriateness of the variables characterizing the data and taxonomic representation in the data-set.

9.1. Reliability of Mouthpart-Morphology Data Sources

In Section 5.2, I have listed the criteria for acceptance of mouthpart-morphology data from the literature. In two-thirds of the taxa examined, I have used two or more references for evaluating head and mouthpart characters; an average of 2.7 references is listed for each taxon in Appendix B. The hexapod mouthpart and head literature that I consulted is sufficiently vast that by using alternative sources that provide descriptions of the same taxon, it was possible to exclude occasional descriptive accounts based on archetypes, generalized abstractions, or imprecise renderings of structure (see Section 6.2). In some instances errors of morphological nomenclature were promulgated from author to author, but rarely were the misnamed structures detected incorrectly in drawings or in the text. Since the mouthpart structure being evaluated is at a coarse-grained level, minor variations in shape, size or structure of particular mouthpart and head elements--variations that would be crucial for evolutionary studies at lower taxonomic levels--are nevertheless immaterial to this study. In summary, given the level of analysis of structure in this study, the reliability of mouthpart data sources is considered high.

9.2. Reliability of Characters Used

I have provided a broad selection of obvious macroscopic features of the head and mouthparts that have direct and indirect associations with feeding (see Chapter 5 for character-by-character summaries). I have deliberately kept the character-states of the characters in a multistate format, thus giving equal weight to all characters irrespective of the number of constituent character-states. I have attempted to use only those features of the head and mouthparts that are functionally linked to process-related aspects of feeding. Although characters were initially selected to minimize intercharacter overlap, some of the characters form correlated character complexes that may give preferential weighting to particular character groups. This is viewed as a positive result of including only those characters that have presumably multidimensional associations with feeding.

The issue of homology is mostly addressed by the phenetic nature of this study, which is concerned with how mouthpart and head structures are deployed as characterizable, nonevolutionary units, regardless of the embryologic origin of those structures. This is in contrast to phylogenetic studies that presuppose an accurate recognition of homology to derive patterns of genealogical descent. Parenthetically, given the above justification, it nevertheless appears that there are homologous character-states for virtually all of the characters analyzed in this study (Snodgrass 1935, Matsuda 1965).

9.3. Taxonomic and Morphologic Representation

The taxonomic representation of hexapods in the data-set is limited by the particular preferences for described hexapod mouthpart structure in the primary and secondary literature. From a survey of Appendix B, it is clear that not all insect groups were sampled evenly (Table 4). Several biases have determined which insect species are worthy of mouthpart and head descriptions. These biases include (i) agriculturally or domestically important pest species, (ii) commonly occurring species in geographic regions intensively sampled by entomologists and (iii) species of particular phylogenetic interest, including "living fossils" and species structurally intermediate between two higher-level taxa. Although I have sampled only 0.15% of extant insect diversity (Tables 4 and 5, Appendix D), I have nevetheless included representatives from 70% of all extant insect families (see Section 6.1). I have attempted to broaden my coverage to include a diverse assemblage of insects, including a concerted attempt to include members of rare groups that bear mouthpart elements unique within their larger taxonomic group. Given the presence of unusual mouthparts in such diminutive, inconspicuous and rare hexapodan groups as proturans and various stylate coleopterans, or in larger sized forms such as a few genera of tropical nocturnal moths, there probably exist mouthpart classes that are undescribed in the literature and not represented in this study. Undescribed groups probably occur as small, cryptic forms occurring in undersampled regions of the world, such as small beetles and flies, and possibly apterygotan groups; parasitic forms are especially suspect. Additionally, if several major insect groups of the Late Paleozoic were analyzed in this study, they would undoubtedly yield distinct mouthpart types. These include the unique stylate-haustellate mouthparts of four orders of Palaeodictyopteroidea and the mandibulate mouthparts of the Protorthopteran family Geraridae (Carpenter 1977, Kukalová-Peck 1987).

CHAPTER 10

SUMMARY AND CONCLUSIONS

In this section I will first sumarize the salient results of my analysis of hexapod mouthpart structure. This will be followed by brief discussions of the importance of holometaboly in the evolution of major mouthpart design and the ubiquity of convergence within mouthpart classes. I will close with a few suggestions for future research.

10.1. Basic Patterns Shown in the Results

1. A phenetic analysis of head and mouthpart structures of 1365 hexapod species, representing all taxonomic orders and 70% of all families, has revealed the presence of 34 basic mouthpart types, each which is characterized by a unique ensemble of structural features. Each mouthpart class is interpreted as comprising a singular solution toward the consumption of a particular food resource. These mouthpart classes are grouped into more inclusive units, based on functional similarities of the included classes.

2. There are moderate to strong associations between mouthpart class and diet type of the included taxa. While some classes have a seemingly obligate requirement of a particular diet type (for example, tristylates and blood, siphonates and sugary solutions), others admit of a much broader range of food (such as consumption by generalized ectognathates of virtually any nutritionally rewarding food and many

fluid foods). In addition to the mouthpart-type/diet association, there are mouthpart-type/functional-feeding-group associations. Mouthpart/feeding group associations can exhibit one-to-one correspondences, multiple feeding groups per mouthpart class, or multiple mouthpart classes per feeding group. This tripartite relationship of mouthpart class, dietary spectrum and functional-feeding-group constitutes the three essential elements in the immediate food acquisition system of hexapods. Because of these associations, mouthpart type can be considered as a proxy for diet or functional-feeding type when the latter categories are unknown. Practical application of these relationships include the categorization of modern insect guilds by examining mouthpart structure from broad-spectrum sampling techniques (such as canopy fogging), or the macroevolutionary history of insect partitioning of dietary resources by the characterization of mouthpart structures in well-preserved deposits.

3. The geochronological record of the development of hexapod mouthpart complexity comprises six major steps. First, by Early Devonian times, primitive entognathous mandibulate and specialized stylate-nonhaustellate mouthparts were in existence. Second, by the Late Carboniferous there was an expansion of several mandibulate mouthpart types and the first appearance of stylate-haustellate mouthparts in winged, paurometabolous insects. Third, after the contraction of swamp forest communities and the increasing aridity of the Permian, various hemipteroid and holometabolous insect groups appeared, replete with distinctive stylate-haustellate mouthparts that probed for shallow-

and deep-seated fluid foods. At this time there were modifications of the typical mandibulate groundplan that was co-opted into filter-feeding and suctorial-predaceous mouthparts among larvae and among minor fluid-feeding mouthparts among adults. Fourth, during the Late Triassic to Middle Jurassic a dipteran radiation occurred and produced a proliferation of several stylate-haustellate mouthpart classes involved with sanguinivory or insectivory. Fifth, during the Late Jurassic to Early Cretaceous, but predating angiospermy, various highly stereotyped fluid- and particle-feeding mouthpart types appeared. Although these mouthpart classes are currently coevolved with angiosperms, their existence during the Jurassic and earliest Cretaceous provides evidence for the lack of original coadaptation with angiosperm plants and favors the hypothesis of subsequent phyletically lateral sequestering by angiosperms of mouthpart types and feeding styles that were already coadapted with pre-existing nonflowering seed plants. Also, there has been a change of some stylate-haustellate groups to feeding on mammalian blood as ectoparasites at least during the early Tertiary and probably earlier.

4. There is good evidence for the decoupling of family-level taxonomic evolution from mouthpart class structural evolution for hexapods during the Early and Middle Mesozoic. This disparity between rate of taxonomic diversification of evolutionary lineages (relatively low) and origination of major feeding structures (relatively high) supports the ecological saturation hypothesis over the expanding resources hypothesis for the modern insect fauna.

10.2. The Role of Metamorphosis in Mouthpart Diversity

In the data summarized in Figs. 131 to 133, there are eight mouthpart classes that are exclusively or dominantly the immature stages of insects; they comprise 24% of the total. Of these, three belong to various aquatic naiads or larvae (pectinate, mouthbrush and mandibulo-brustiate) and the other five are restricted to terrestrial larvae of various holometabolous groups. These distinctive mouthpart types are apparently a consequence of the ecological decoupling of the immature from the adult life-stages in insects, even in paleopterans, which lack a larval stage but exhibit dramatic differences in habitat occupation between aquatic naiads and terrestrial adults, and in holometabolic forms, which bear a well-differentiated, active larva that is separated from the adult stage by a resting stage, the pupa.

The earliest evidence for holometaboly in the fossil record has been various neuropteroid, coleopteran and mecopteran fossils, mostly wings, from Lower Permian deposits of North America and Asia (Rohdendorf and Rasnitsyn 1980, Wootton 1981, Carpenter and Burnham 1985). However, many researchers have voiced suspicions that holometaboly must have originated during the Carboniferous (Carpenter 1953, Ross et al. 1982, Whalley 1986) and recent body- and trace-fossil evidence has provided corroboration for these claims (Kukalová-Peck 1988, Labandeira and Beall 1990).

There has also been a corollary claim, from indirect evidence, that the larval stages of the earliest holometabolans were physically small (Carpenter 1953). Given a spatiotemporal disjunction between the immature and adult stages and the consumption of unique and probably novel food resources by small larval forms, the presence of special mouthpart apparati seems inescapable. These specialized mouthpart types include in the modern fauna mouthparts as diverse as three classes designed for entrapping suspended particulate matter in water (pectinate, mandibulobrustiate and mouthbrush); one class among leaf-miners with sawblade or picklike mandibles that cut through leaf mesophyll (sericterate); and three classes characterized by tubulate mandibles or mandible/maxillary complexes for predatory, piercing-and-sucking carnivory (fossate-complex, tubulomandibulate, mouthhook). Thus the spatiotemporal separation of the immature from the adult stage and the accompanying consequence of resource partitioning of qualitatively different foods resulted in a significant addition to the roster of mouthpart classes.

Because of the lack of functional wings in the immatures, the two ecologically distinctive lifestyles alluded to above have been not only been produced but actively maintained. Larval stages are tied to substrata where dispersal is relatively unimportant for securing food resources whereas the adult stage of the same taxa are mostly plant herbivores or consumers of plant herbivores in terrestrial, seed-plant dominated ecosystems. For different reasons many adult holometabolous insects have developed mouthparts to handle the unique products of these terrestrial ecosystems, namely those produced by seed plants, including spores and pollen (adult-ectognathates, siphonates), nectar (glossates, labellates, siphonates) and wood (rhynchophorates).

10.3. The Phenomenon of Convergence

The incorporation of multiple monophyletic lineages within many mouthpart classes is a major conclusion of this study. When the 34 mouthpart classes are mapped onto phylogenetic trees of members comprising each class, two major patterns are evident (see phylograms of Section 8). Several mouthpart classes are coincident with monophyletic groups (raptorial-ectognathate, fossate-complex, tristylate). Others contain groups that are taxonomically disparate (adult-ectognathate, ectognathous-stylate, reduced-trophic). (I have presented 78 examples of mouthpart convergence in Table 8.)

These patterns lend support to the hypothesis that there are only a limited number (herein determined as 34) of fundamental ways to procure food among terrestrial hexapods. These fundamental ways apparently have fixed structural requirements on mouthpart apparati, such that unrelated taxa often co-opt homologous or analogous elements that result in mouthparts that are structurally and functionally equivalent.

A more fundamental question, however, is what phenomenon underpins this pervasive pattern of structural and functional convergence. I propose that mouthpart convergence is related to (i) the fundamental properties of terrestrial and freshwater food, particularly its form (solid, liquid or particulate) and (ii) the distribution of this form among tissue types that are consumed. The first aspect is largely responsible for the occurrence of mouthpart series, particularly mandibulate and nonmandibulate mouthparts. Fluid-feeding, a condition derived from mandibulate mouthparts, has in turn generated a greater structural diversity in hexapods at the mouthpart-class level.

10.4. Mouthpart Aptation and the Success of Insects

The success of insects have historically been attributed to the frequently-cited features of the presence of an exoskeleton, flight and developmental metamorphosis (see Chapter 2 for discussion). However when each of these innovations are examined individually, they are not unique to insects. Vertebrates, for example, have evolved flight and developmental metamorphosis in several clades; other considerably less diverse terrestrial arthropods possess chitinized exoskeletons and the relative small size that it confers. Instead of focusing on structural features *per se*, an alternative tack is to consider the single ecological context where insects are most diverse. Undoubtedly this context is the myriad plant-feeding associations that have been established between (mostly holometabolous) insects and (mostly angiospermous) seed plants.

The combined species diversities of the two most dominant terrestrial clades--holometabolous insects and angiosperm plants--essentially structure most present-day terrestrial ecosystems. The causes of this inflation in diversity lies in the intricate and highly stereotyped modes that insects use to partition food resources in seed plants in general and angiosperms in particular. There is not only a general sequestering of food resources by insects based on various biologically-enclosed organ tissues, but also an accessing of surface-exposed products of some of those tissues such as nectar, oils, pollen, resin and exuding sap. The multitude of these discrete and diverse food resources has been collectively and near-totally exploited by the only terrestrial clade of animals that possess the requisite trophic structures for its consumption: insects. Requisite insect modifications include the presence of five major mouthpart regions (clypeus/labrum, "pharyngeal" region, mandibles, maxillae, labium) most of which bear appendicular lobes and/or multisegmented palps as well as various co-optations of elements within and between regions for the co-ordinated procurement, manipulation, processing and ingestion of food. The processing of food can take the form of simple mastication by gnathal segments, fluid-pumping from stylets, sponging from conjoined galeae or lapping by a prolonged, hirsute glossa. Whereas a limited number of vertebrates perform some of these feeding strategies (Owen 1980), they are not as successful as insects when measured by the diversity of subclades that can perform these strategies or their pervasiveness in ecosystems (Armstrong 1979, Barth 1985).

A conclusion of this study is that the complexity of insect mouthparts, both in terms of mouthpart regions and elements within mouthpart regions, has led to insect success. This success became manifest when seed plants in general and angiosperms in particular present externally-exposed food resources that were exploited in several fundamentally different ways by various insect clades during the middle Mesozoic. Vertebrates have achieved a much more limited repertoire of consuming some of these same food resources by modifications of a comparatively simple mouthpart system (essentially a single pair of dorsoventrally positioned jaws). It appears that insect success is largely attributable to the maintenance of generalized mandibulate clades, each with the primitive and complex complement of mouthparts, and the subsequent, serial derivation in various subclades of more modified structures for consumption of "atypical," specialized seed plant products. These seed plant products notably include foods in fluid and particulate form, which incurs new mouthpart modifications for consumption. Thus both structural and taxonomic diversity of holometabolous insects has increased in tandem with the rise of seed plant external and internal anatomic complexity. (See Fig. 135 for an approximation of this pattern by use of mouthpart class as a proxy for seed plant tissue type complexity.)

10.5. Future Research

This study is a preliminary, coarse-grained examination of the wealth of structural diversity in modern hexapod mouthparts. However, there are two major consequences of this study that are relevant to the study of the origin, evolution and current diversity of hexapod trophic roles. First is the establishment of an explicit criterion for recognition of feeding guilds in studies of Recent insect communities. Since Root's (1967) formal definition of a guild as a "group of species that exploit the same class of resources in a similar way," there has been considerable confusion regarding application of the term (Terbough and Robinson 1986, Hawkins and MacMahon 1989), particularly in entomological studies, where the term is frequently used congruently with taxonomic units (e.g. Hajek and Dahlsten 1986, Flamm et al. 1989). However, it is clear that many insect feeding guilds do not each have the same taxonomic common denominator (Hawkins and MacMahon 1989) and reference to a taxonomically independent yet ecologically relevant parameter is sorely needed. Definition of a guild in terms of a particular mouthpart class and with reference to a particular dietary resource may often provide a more precise operational guideline in use of the term "guild" in ecological entomology.

Second, one of the most perplexing yet understudied aspects of the macroevolutionary development of hexapods has been their steady dominance of all consumer trophic roles in terrestrial and freshwater ecosystems. Virtually all studies investigating the origin and evolution of hexapodan dietary partitioning of the post-Silurian world have focused on biogeographical and taxonomic studies of host-plant/insect associations and the geochronologic extension of the derived patterns (e.g. Zwölfer 1978, Mitter et al.1988). An independent approach that could document the timing of invasion of new food-resource zones in the historical record is interpretation of hexapod mouthpart structure and diet assignment in selected, well-preserved *Lagerstätten* deposits. Corroborative evidence could be supplied by documentation of insect damage on fossil plant material, characterization of insect gut contents, and examination of insect coprolites. These approaches, used in conjunction with each other, would go far in promoting understanding of how it was that hexapods, and insects in particular, became the most diverse organismic group of all time consuming virtually every nutritionally-rewarding food resource in terrestrial and freshwater ecosystems.

THE UNIVERSITY OF CHICAGO

USE OF A PHENETIC ANALYSIS OF RECENT HEXAPOD MOUTHPARTS FOR THE DISTRIBUTION OF HEXAPOD FOOD RESOURCE GUILDS IN THE FOSSIL RECORD

VOLUME FOUR

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE PHYSICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
DEPARTMENT OF GEOPHYSICAL SCIENCES

BY
CONRAD CHRISTOPHER LABANDEIRA

CHICAGO, ILLINOIS
AUGUST, 1990

REFERENCES CITED

Abdullah, M. 1965. New Anthicidae and Pyrochroidae (Coleoptera) from Baltic amber (Oligocene). *Entomologist*, 98: 38-42.

Abdullah, M. 1975. The higher classification of the insect order Coleoptera including fossil records and a classified directory of the coleopterists and Coleoptera collections of the world. *Zool. Beit.*, N.F., 21: 363-461.

Abrahamson, W.G. 1989. Plant-animal interactions: an overview. IN: Abrahamson, W.G., (Ed.), *Plant-Animal Interactions*, pp. 1-22. New York: McGraw-Hill Book Co.

Achtelig, M. 1967. Uber die Anatomie des Kopfes von *Raphidia flavipes* Stein und die Verwandtschaftsbeziehungen der Raphidiidae zu den Megaloptera. *Zool. Jb. (Anat.)*, 84: 249-312.

Acker, T.S. 1958. The comparative morphology of *Stenorrhachus walkeri* (McLachlan) and of *Nemopterella* sp. (Neuroptera: Nemopteridae). *Microentomology*, 23: 106-114.

Aczel, M.L. 1955. Nothybidae, a new family of Diptera. *Treubia*, 23: 1-18.

Aczel, M.L. 1961. A revision of American Neriidae (Diptera, Acalyptratae). *Studia Entomol.*, 4: 257-346.

Adams, E.C.G. and Salmon, J.T. 1972. The mouth-parts and feeding methods of *Brachystomella parvula* (Schaeffer) (Collembola: Brachystomellidae. *Trans. Roy. Entomol. Soc. London*, 124: 269-286.

Adams, P.A. 1967. A review of the Mesochrysinae and Nothochrysinae (Neuroptera: Chrysopidae). *Bull. Mus. Comp. Zool.*, 135: 215-238.

Aderkas, P. von and Peterson, B.V. 1987. Chirosia betuleti (Ringdahl) (Diptera: Anthomyiidae) a gall-former on the ostrich fern, *Matteuccia struthiopteris*, with notes on other insect-fern associates. *Proc. Entomol. Soc. Washington*, 89: 532-647.

Adis, J. and Sturm, H. 1987. On the natural history and ecology of Meinertellidae (Archaeognatha, Insecta) from dryland and innundation forests of central Amazonia. *Amazoniana*, 10: 197-210.

Adler, S. and Theodor, O. 1926. The mouth parts, alimentary tract, and salivary apparatus of the female in *Phlebotomus papatsii*. *Ann. Trop. Med. Parasitol.*, 20: 109-142.

d'Aguilar, J. 1944. Contribution à la étude des Phalacridae: note sur *Phalacrus caricis*. *Ann. Epiph.*, 10: 85-91.

Ahmad, M. 1943. The morphology and biology of *Rhogas testaceus* (Spin.) a braconid internal parasite of spotted bollworms of cotton. *Indian J. Entomol.*, 5: 189-205.

Ahmad, M. 1950. The phylogeny of termite genera based on imago-worker mandibles. *Bull. Am. Mus. Nat. Hist.*, 95: 37-86.

Akbar, S. 1957. The morphology and life-history of *Leptocorisa varicornis* Fabr. (Coreidae, Hemiptera)--a pest of paddy crop in India. *Aligargh Muslim Univ. Publ. (Zool. Ser.), Indian Insect Types*, 5: 1-53.

Alam, S.M. 1952. A contribution to the biology of *Stenobracon dessae* Cameron (Braconidae, Hymenoptera), and the anatomy of its preimaginal stages. *Z. Parasitol.*, 15: 159-182.

Aldrich, J.M. 1922. A new genus of two-winged fly with mandible-like labella. *Proc. Entomol. Soc. Washington*, 24: 145-148.

Alexander, C.P. 1931. Crane-flies of the Baltic amber (Diptera). *Bernstein-Forsch.*, 2: 1-135.

Alexander, C.P. 1937. Family Tipulidae. IN: Carpenter, F.M., (Ed.), Fossils insects from the Creede Formation, Colorado. Part 1. Introduction, Neuroptera, Isoptera, and Diptera. *Psyche*, 45:110-114.

Alexander, C.P. 1981a. Tanyderidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 149-152.

Alexander, C.P. 1981b. Trichoceridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 301-504.

Alexander, C.P. 1981c. Ptychopteridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 325-328.

Alexander, C.P. and Byers, G.W. 1981. Tipulidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 153-190.

Allen, E.J. and Foote, B.A. 1967. Biology and immature stages of three species of Otididae (Diptera) which have saprophagous larvae. *Ann. Entomol. Soc. Am.*, 60: 826-836.

Allen, E.J. and Foote, B.A. 1975. Biology and immature stages of *Tritoxa incurva* (Diptera: Otitidae). *Proc. Entomol. Soc. Washington*, 77: 246-257.

Almond, J.E. 1985. The Silurian-Devonian fossil record of the Myriapoda. *Trans. Roy. Soc. London*, (B), 309: 227-237.

Aly, C. 1984. Functional morphology of the mouthparts of *Aedes vexans* Meig. larvae (Diptera: Culicidae). *Abstr. 17th Int. Congr. Entomol.*, p. 78.

Ananthakrishnan, T.N. 1979. Biosystematics of Thysanoptera. *Ann. Rev. Entomol.*, 24: 159-183.

Ananthakrishnan, T.N. and James, P.W. 1983. Feeding preferences in some sporophagous Idolothripinae (Tubulifera: Thysanoptera). *Proc. Indian Natl. Acad. Sci.*, (B), 49: 86-92.

Ananthakrishnan, T.N. and Suresh, G. 1983. Patterns of fungal resource utilization and feeding range in some mycophagous Tubulifera (Insecta: Thysanoptera). *Proc. Indian Acad. Sci., (Anim. Sci.)*, 92: 285-291.

Andersen, N.M. 1978. A new family of semiaquatic bugs for *Paraphrynovellia* Poisson with a cladistic analysis of relationships. *Steenstrupia*, 4: 211-225.

Andersen, N.M. 1982. The semiaquatic bugs (Hemiptera Gerromorpha). Phylogeny, adaptations, biogeography and classification. *Entomonograph*, 3: 1-454.

Andersen, N.M. and Polhemus, J.T. 1976. Water-striders (Hemiptera: Gerridae, Veliidae, etc.). IN: Cheng, L., (Ed.), *Marine Insects*, pp. 187-224. Amsterdam: North-Holland Publ. Co.

Andersen, N.M. 1982. A fossil water measurer (Insecta, Hemiptera, Hydrometridae) from the Paleocene/Eocene of Denmark and its phylogenetic relationships. *Bull. Geol. Soc. Denmark*, 30: 91-96.

Anderson, D.T. 1959. The embryology of the polychaete *Scolopos armiger*. *Quart. J. Microsc. Sci.*, 100: 89-166.

Anderson, D.T., Fletcher, M.J. and Lawson-Kerr, C., 1976. A marine caddis fly, *Philanisus plebeius*, ovipositing in a starfish, *Patiriella exigua*. *Search*, 7 : 483-484.

Anderson, D.T. and Lawson-Kerr, C., 1977. The embryonic development of the marine caddis fly, *Philanisus plebeius* Walker (Trichoptera: Chathamidae). *Biol. Bull.*, 153: 98-105.

Anderson, N.H. and Wallace, J.B. 1984. Habitat, life history, and behavioral adaptations of aquatic insects. IN: Merritt, R.W. and Cumnmins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 38-58. Dubuque: Kendall/Hunt Publ. Co.

Anderson, N.H. and Cargill, A.S. 1987. Nutritional ecology of aquatic detritivorous insects. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 903-925. New York: John Wiley and Sons.

Anderson, W.H. 1936. A comparative study of the labium of coleopterous larvae. *Smithson. Misc. Collns.*, 95: 1-29.

Anderson, W.H. 1941. On some larvae of the genus *Proterorhinus* (Coleoptera: Aglycyderidae). *Proc. Hawaiian Entomol. Soc.*, 11: 25-35.

Anschau, M. 1950. Uber eine Eigentumlichkeit im Bau der larvalen Mandibeln beim grossen Kolbenwasserkafer (*Hydrous piceus* L.) und deren biologische Bedeutung. *Oster. Zool. Z.*, 2: 275-281.

Anthon, H. 1943a. Der Kopfbau der Larven einiger nematoceren Dipterenfamilien: Rhyphidae, Trichoceridae, Psychodidae und Ptychopteridae. *Spolia Zool. Mus. Hauiensis*, 3: 7-61, pls. 1-11.

Anthon, H. 1943b. Zum Kopfbau der primitivsten bisher bekannten Dipterenlarvae: *Olbiogaster* sp. (Rhyphidae). Ein Beitrag zur Phylogenie der nematoceren Dipteren. *Entomol. Medded.*, 23: 303-320, pls. 1-3.

Anthony, M.H. 1902. The metamorphosis of *Sisyra*. *Am. Nat.*, 36: 615-630.

Appanah, S. and Chan, T.H. 1981. Thrips: pollinators of some dipterocarps. *Malay. Forester*, 44: 234-252.

Applegarth, A.G. 1939. The larva of *Apterobittacus apterus* MacLachlan (Mecoptera: Panorpidae). *Microentomology*, 4: 109-120, figs. 52-58.

Applegarth, A.G. 1952. The anatomy of the cephalic region of a centipede *Pseudolithobius megaloporus* (Stuxberg) (Chilopoda). *Microentomology*, 17: 127-171.

Aristotle, *Historia Animalium*. IN: Adler, M.,(Ed.), *Great Books of the Western World*, 9: 3-158. Chicago: Encyclopaedia Brittanica.

Aristotle, *De Partibus Animalium*. IN: Adler, M., (Ed.), *Great Books of the Western World*, 9: 159-229. Chicago: Encyclopaedia Brittanica.

Armbruster, L. 1929. Versteinerte Honigbienen aus dem obermiocänen Randecker Maar. *Arch Bienk.*, **19**: 97-133.

Armstrong, J.A. 1979. Biotic pollination mechanisms in the Australian flora--a review. *New Zealand J. Bot.*, **17**: 467-508.

Arnett, R.H., Jr. 1963. *The Beetles of the United States*. Washington, D.C.: Catholic University of America Press. 1112 p.

Arnett, R.H., Jr. 1985. *American Insects: A Handbook of the Insects North of Mexico*. New York: Van Nostrand-Reinhold Co. 850 p.

Arnett, R.H., Jr. and Jacques, R.L., Jr. 1981. *Simon and Schuster's Guide to Insects*. New York: Simon and Schuster. 512 p.

Arnett, R.H., Jr. and Jacques, R.L., Jr. 1985. *Insect Life: A Field Entomology Manual for the Amateur Naturalist*. Englewood Cliffs, N.J.: Prentice-Hall. 354 p.

Arnoldi, L.V. 1977. Rhynchophora, Eobelidae. IN: Arnoldi, L.V., Nitrikin, L.M., Zherikin, V.V. and Ponomarenko, A.G., (Eds.), "Mesozoic Coleoptera." *Trans. Paleontol. Inst.* **161**: 142-146.

Arnoldi, L.V., Nitrikin, L.M., Zherikin, V.V. and Ponomarenko, A.G. 1977. Mesozoic Coleoptera. *Trans. Paleontol. Inst.*, **161**: 1-204.

Arora, G.L. 1959. External morphology of the larva of *Diprion pini* (L.) (Symphyta: Hymenoptera). *Res. Bull. Punjab Univ.*, N.S., **10**: 55-64.

Arora, G.L. and Singh, S. 1962. Morphology and musculature of the head and mouth-parts of *Idiocerus atkinsoni* Leth. (Jassidae, Homoptera). *J. Morphol.*, **110**: 131-140.

Asahina, S. 1950. On the life history of *Epiophlebia superstes* (Odonata, Anisozygoptera). *Proc. 8th Int. Congr. Entomol.*, pp. 337-341.

Asahina, S. 1954. *A Morphological Study of a Relic Dragonfly, Epiophlebia Superstes Selys (Odonata, Anisozygoptera)*. Tokyo: Japan Soc. Prom. Sci. 153 p., 70 pls.

Ashbourne, S.R.C. and Putman, R.J. 1987. Competition, resource partitioning and species richness in the phytophagous insects of red oak and aspen in Canada and the U.K. *Acta Oecol.*, **8**: 43-56.

Ashe, J.S. 1981. Studies of the life history and habits of *Phanerota fasciata* Say (Coleoptera: Staphylinidae: Aleocharinae) with notes on the mushroom as a habitat and descriptions of the immature states. *Coleopt. Bull.*, 35: 83-96.

Ashe, J.S. 1982. Evidence about species status of *Phanerota dissimilis* (Erichson) (Coleoptera: Staphlylinidae: Aleocharinae) from host mushroom relationships. *Coleopt. Bull.*, 36: 155-161.

Ashe, J.S. 1984a. Major features of the evolution of relationships between gyrophaenine staphylinid beetles and fresh mushrooms. IN: Wheeler, Q., and Blackwell, M., (Eds.), *Fungus/Insect Relationships: Perspectives in Ecology and Evolution*, pp. 227-255. New York: Columbia University Press.

Ashe, J.S. 1984b. Generic revision of the subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with a review of the described subgenera and major features of evolution. *Quaest. Entomol.*, 20: 129-349.

Ashford, R.W. 1970. Observations on the biology of *Hemimerus talpoides* (Insecta: Dermaptera). *J. Zool.*, 33: 191-195.

Ashton, P. 1977. A contribituon of rain forest research to evolutionary theory. *Ann. Missouri Bot. Gard.*, 64: 694-705.

Atkins, M.D. 1978. *Insects in Perspective*. New York: Collier-Macmillan Publishing Co. 513 p.

Austen, E.E. 1936. A remarkable semi-apterous fly (Diptera)found in a cave in East Africa, and representing a new family, genus and species. *Proc. Zool. Soc. London*, 1936: 425-431.

Awati, P.R. 1914. The mechanism of suction in the potato capsid bug, *Lygus pabulinus* Linn. *Proc. Linn. Zool. Soc. London*, 1914: 685-733.

Backus, E.A. 1985. Anatomical and sensory mechanisms of leafhopper and planthopper feeding behavior. IN: Nault, L.F. and Rodriguez, J.G., (Eds.), *The Leafhoppers and Planthoppers*, pp. 163-194. New York: John Wiley and Sons.

Backus, E.A. 1987. Feeding and host selection behaviors of *Empoasca fabae* as compared to other leafhoppers. IN: Wilson, M.R. and Nault, L.R., (Eds.), *Proceedings of the Second International Workshop on Leafhoppers and Planthoppers of Economic Importance*, p. 251. London, CIE.

Backus, E.A. 1988. Sensory systems and behaviours which mediate hemipteran plant-feeding: a taxonomic overview. *J. Insect Physiol.*, 34: 151-165.

Backus, E.A. and McLean, D.L. 1985. Behavioral evidence that the precibarial sensilla of leafhoppers are chemosensory and function in host discrimination. *Entomol. Exp. Appl.*, **37**: 219-228.

Badcock, R.M. 1961. The morphology of some parts of the head and maxillo-labium in larval Trichoptera, with special reference to the Hydropsychidae. *Trans. Roy. Entomol. Soc. London*, 113: 217-248.

Badonnel, A. 1931. Copéognathes de France (11^e note). Sur les pièces buccales de *Scoliopsyllopsis latreillei* (Enderlein). *Bull. Soc. Zool. France*, 56: 250-257.

Badonnel, A. 1934. Recherches sur l'anatomie des psoques. *Bull. Biol. France Belg., Suppl.*, **18**: 1-241.

Badonnel, A. 1936. Sur l'hypopharynx des psoques. *Bull. Soc. Zool. France*, **61**: 14-18.

Badonnel, A. 1951. Ordre des Psocopteres. IN: Grasse, P.P., (Ed.), *Traite de Zoologie*, **10(2)**: 1301-1340. Paris: Paul Masson.

Badonnel, A. and Lienhard, C. 1988. Révision de la famille des Mesopsocidae (Insecta, Psocoptera). *Bull. Mus. Natl. Mus. Nat., Paris*, (4) 10: 375-412.

Baer, H. 1912. Beiträge zur Kenntnis der Thysanuren. *Jen. Z. Naturwiss.*, **48**: 1-92.

Baird, G.C. 1979. Lithology and fossil distribution, Francis Creek Shale in northeastern Illinois. IN: Nitecki, M.H., (Ed.), *Mazon Creek Fossils*, pp. 41-67. New York: Academic Press.

Baird, G.C., Shabica, C.W., Anderson, J.L. and Richardson, E.S., Jr. 1985. Biota of a Pennsylvanian muddy coast: habitats within the Mazonian delta complex, northeast Illinois. *J. Paleontol.*, **59**: 253-281.

Baird, G.C., Sroka, S.D., Shabica, C.W. and Beard, T.L. 1985. Mazon Creek-type fossil assemblages in the U.S. midcontinent Pennsylvanian: their recurrent character and palaeoenvironmental significance. *Phil. Trans. Roy. Soc. London*, (B), **311**: 87-99.

Baker, G.T. and Chan, W.P. 1987. Sensilla on the antennae and mouthparts of the larval and adult stages of *Olethreutes cespitana* (Lepidoptera: Tortricidae). *Ann. Soc. Entomol. France*, N.S., 23: 387-397.

Baker, G.T. and Ellsbury, M.M. 1988. Morphology of the mouth parts and antenna of the larva of the clover stem borer, *Languria mozardi* La Treille (Coleoptera: Languriidae). *Proc. Entomol. Soc. Washington*, **91**: 15-21.

Baker, H.G. 1986. Yuccas and yucca moths--a historical commentary. *Ann. Missouri Bot. Gard.*, **73**: 556-564.

Baker, H.G. and Baker, I. 1980. Studies of nectar constitution and pollinator-plant coevolution. IN: Gilbert, L.E. and Raven, P.H., (Eds.), *Coevolution of Animals and Plants*, pp. 100-140. Austin: University of Texas Press.

Baker, H.G. and Baker, I. 1983. Floral nectar sugar constituents in relation to pollinator type. IN: Jones, C.E. and Little, R.J., (Eds.), *Handbook of Experimental Pollination Biology*, pp. 117-141. Princeton: Van Nostrand-Reinhold.

Baker, H.G. and Hurd, P.D. 1968. Intrafloral ecology. *Ann. Rev. Entomol.*, **13**: 385-414.

Balachowsky, A. 1937. Les cochenilles de France, d'Europe, du nord de l'Afrique et du Bassin Mediterraneen. Caracteres generaux des cochenilles--morphologie externe. *Actual Sci. Indust.*, **526**: 1-67.

Balduf, W.V. 1935. *The Bionomics of Entomophagous Coleoptera*. St. Louis: John S. Swift Co., Inc. 220 p.

Balduf, W.V. 1974. *The Bionomics of Entomophagous Insects*. London: E.W. Classey, Ltd. 384 p.

Balfour-Browne, F. 1922. The life-history of the water-beetle *Pelobius tardus* Herbst. *Proc. Zool. Soc. London*, **1922**: 79-97.

Balfour-Browne, F. 1944. The proventriculus of the Coleoptera (Adephaga) and other insects--a study in evolution. *J. Roy. Microsc. Soc.*, **64**: 68-117.

Ball, A. 1936. Un psoque qui perd un partie de ses pièces buccales en devenant adulte. *Mem. Mus. Roy. Hist. Nat. Belgique*, (2), **3**: 395-399.

Banerji, L.G., 1960. Morphology of the head capsule of *Aspongopus janus* Fabr. (Pentatomidae: Heteroptera). *Agra Univ. J. Res.*, **9**: 47-64.

Banks, C.J. 1939. Cephalic glands in the Corixidae (Hemipt.). *Proc. Roy. Entomol. Soc. London*, (A), **14**: 83-85.

Bänziger, H. 1967. Preliminary observations on a skin-piercing blood sucking moth (*Calyptra eustrigata*) (Hmps.) (Lepid., Noctuidae) in Malaya. *Bull. Entomol. Res.*, 58: 159-163, pls. 1-10.

Bänziger, H. 1970. The piercing mechanism of the fruit-piercing moth *Calpe* (*Calyptra*) *thalictri* Bkh. (Noctuidae) with reference to the skin-piercing blood-sucking moth *C. eustrigata* Hmps. *Acta Trop.*, 27: 54-88.

Bänziger, H. 1971. Bloodsucking moths of Malaya. *Fauna*, 1: 3-16.

Bänziger, H. 1971. Extension and coiling of the lepidopterous proboscis--a new interpretation of the blood-pressure theory. *Mitt. Schweiz. Entomol. Ges.*, 43: 225-239.

Bänziger, H., 1972. Biologie der lacriphagen Lepidopteren in Thailand und Malaya. *Rev. Suisse Zool.*, 79: 1381-1469.

Bänziger, H., 1975. Skin-piercing blood-sucking moths I: Ecological and ethological studies on *Calpe eustrigata* (Lepid., Noctuidae). *Acta Trop.*, 32: 125-144.

Bänziger, H. 1979. Skin-piercing blood-sucking moths II: Studies on a further 3 adult *Calyptra* (*Calpe*) sp. (Lepid., Noctuidae). *Acta Trop.*, 36: 23-37.

Bänziger, H. 1980. Skin-piercing blood-sucking moths III: Feeding act and piercing mechanism of *Calyptra eustrigata* (Hmps.) (Lep., Noctuidae). *Mitt. Schweiz. Entomol. Ges.*, 53: 127-142.

Bänziger, H., 1982. Fruit-piercing moths (Lep., Noctuidae) in Thailand: a general survey and some new perspectives. *Bull. Soc. Entomol. Suisse.*, 55: 213-240.

Bänziger, H., 1983. Lachryphagous Lepidoptera recorded for the first time in Laos and China. *Bull. Soc. Entomol. Suisse*, 56: 73-82.

Bänziger, H., 1985. Description of three new lachryphagous moths of the genus *Mabra* from Thailand, Malaysia, and China (Lepidoptera: Pyralidae). *Bull. Soc. Entomol. Suisse*, 58: 23-30.

Bänziger, H., 1986. Skin-piercing blood-sucking moths IV: biological studies on adults of 4 *Calyptra* species and 2 subspecies (Lep., Noctuidae). *Bull. Soc. Entomol. Suisse*, 59: 111-138.

Barbier, R. 1961, Contribution a l'etude de l'anatomie sensorinerveuse des insectes Trichopteres. *Ann. Sci. Nat. Zool.*, 3: 173-183.

Barbosa, P. and Wagner, M.R. 1989. *Introduction to Forest and Shade Tree Insects*. New York: Academic Press, Inc. 639 pp.

Baroni-Urbani, C. and Saunders, J.B. 1982. The fauna of the Dominican Republic amber: the present status of knowledge. *Mem. Ninth Caribbean Geol. Conf.*, 1: 213-223.

Barraud, P.J. and Covell, M.G. 1928. The morphology of the buccal cavity in anopheline and culicine mosquitoes. *Indian J. Med. Res.*, 15: 671-679, pls. 60-67.

Barth, F.G. 1985. *Insects and Flowers: The Biology of a Partnership.* Princeton, N.J.: Princeton Univ. Press. 297 p.

Barth, R. 1952. Estudos anatomicos e histologicos sobre a subfamilia Triatominae (Heteroptera, Reduviidae). I parte: A cabeça do *Triatoma infestans*. *Mem. Inst. Oswaldo Cruz*, 5: 69-196.

Barth, R. 1953. Estudos anatomicos e histologicos sobre a subfamilia Triatominae (Heteroptera, Reduviidae). III parte: Pesquisas sobre o mecanismo da picada dos Triatominae. *Mem. Inst. Oswaldo Cruz*, 51: 11-72.

Barthel, M. and Hetzer, H. 1982. Bernstein-Inklusen aus dem Miozän des Bitterfelder Raumes. *Z. Angew. Geol.*, 28: 314-336.

Barthel, M. and Jablonski, D. 1979. Solnhofen formation. IN: Fairbridge, R.W. and Jablonski, D., (Eds.), *The Encyclopedia of Paleontology*, pp. 757-764. Stroudsburg, PA: Dowden, Hutchinson and Ross, Inc.

Baudoin, R. 1980. Sur les *Gerris* miroirs d'eau actuels et les *Chresmoda* de lagunes postrecifales portlandiennes de Solnhofen. *Ann. Sci. Nat., Zool.*, (13), 3: 111-116.

Bauer, T. and Kredler, M. 1988. Adhesive mouthparts in a ground beetle larva (Coleoptera, Carabidae, *Loricera pilicornis* (F.) and their function during predation. *Zool. Anz.*, 221: 145-156.

Baumann, R.W. 1982. Plecoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 389-393. New York: McGraw-Hill.

Beardsley, J.W. 1968. External morphology of the adult male of *Matsuococcus bisetosus*. *Ann. Entomol. Soc. Am.*, 61: 1449-1459.

Beardsley, J.W. 1969. A new fossil scale insect (Homoptera: Coccoidea) from Canadian amber. **Psyche**, 76: 270-279.

Becker, E. 1929. Zum Bau des Kopfes der Rhynchoten. *Rev. Zool. Russe*, 9: 54-96.

Beier, M. 1952. Bau und funktion der Mundwerkzeuge bei den Helodidenlarven (Col.). *Trans. 9th Int. Congr. Entomol.*, 1:135-138.

Beier, M. 1955. Embioidea und Orthopteroidea. IN: Bronns, H.G., (Ed.), *Klassen und Ordnungen des Tierreichs*, 5 (Abt. 3, Buch 6): 1-304.

Beier, M. 1972. Saltatoria (Grillen und Heuschrecken). IN: Beier, M., (Ed.), *Handbuch der Zoologie*, 4 (Hälfte 2, Teil 2): 1-217.

Beirne, B.P. 1941. A consideration of the cephalic structures and spiracles of the final instar larvae of the Ichneumonidae (Hym.). *Trans. Soc. Brit. Entomol.*, 7: 123-190.

Bekker-Migdisova, E.E. 1940. Fossil Permian insects. *Trans. Paleontol. Inst.*, 11: 1-98, pls. 1-6.

Bekker-Migdisova, E.E. 1959. Some new important groups of Sternorrhyncha from the Permian and Mesozoic of the USSR. *Materials and Fundamentals of Paleontology*, 3. Moscow: Academy of Science. [In Russian.]

Bekker-Migdisova, E.E. 1960. New Permian Homoptera from the European USSR. *Trans. Paleontol. Inst.*, 76: 1-112. [In Russian.]

Bekker-Migdisova, E.E. 1961. Psocopteroidea, Rhynchota. IN: Rohdendorf, B.B., Bekker-Migdisova, E.E., Martynova, O.M. and Sharov, A.G., "Paleozoic Insects from the Kusnetsk Basin." *Trans. Paleontol. Inst.*, 85: 271-393. [In Russian].

Bekker-Migdisova, E.E. 1968. Protopsyllidids and their morphology. IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 87-98. Moscow: Academy of Sciences. [In Russian].

Bekker-Migdisova, E.E. 1985. Fossil insect Psyllomorpha. *Trans. Paleontol. Inst.*, 206: 1-93, pls. 1-16. [In Russian.]

Beklemishev, V.N. 1957. Some general questions on the biology of bloodsucking lower flies. *Medit. Parasitol. Parasitar. Bol.*, 5: 562-566. [In Russian.]

Bennack, D.E. 1981. The effects of mandible morphology and photosynthetic pathway on selective herbivory in grasshoppers. *Oecologia*, 51: 281-283.

Bennett, G.F. 1955. Studies on *Cuterebra emasculator* Fitch 1956 (Diptera: Cuterebridae) and a discussion of the status of the genus *Cephenemyia* Ltr. 1818. *Can. J. Zool.*, 33: 75-98.

Benwitz, G. 1956. Der Kopf von *Corixa punctata* Ill. (*geoffroyi* Leach) (Hemiptera, Heteroptera). *Zool. Jb. (Anat.)*, 75: 311-378.

Bequaert, J. 1932. The Nemestrinidae (Diptera) in the V.V. Roder Collection. *Zool. Anz.*, 100: 13-33.

Bequaert, J. and Carpenter, F.M. 1936. The Nemestrinidae of the Miocene of Florissant, Colorado, and their relations to the Recent fauna. *J. Paleontol.*, 10: 395-409.

Berland, L. 1947. Hymenopteres Tenthredoides. *Faune de France*, 47: 1-496. Paris: Paul Lechevalier.

Berlese, A. 1909. Morfologia generale. IN: Berlese, A., *Gli Insetti*, 1: 64-163. Milan: Societa Editrice Libraria.

Bernard, J. 1974. Mecasime d'ouverture de la bouche chez l'hemiptere hematophage, *Triatoma infestans*. *J. Insect Physiol.*, 20: 1-8.

Bernays, E.A. 1981. Plant tannins and insect herbivores: an appraisal. *Ecol. Entomol.*, 6: 353-360.

Bernays, E.A. 1986. Diet-induced head allometry among foilage-chewing insects and its importance for graminivores. *Science*, 231: 495-497.

Bernays, E.A. and Barbehenn, R. 1987. Nutritional ecology of grass foilage-chewing insects. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 147-175. New York: John Wiley and Sons.

Bernays, E. and Graham, M. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology*, 69: 886-892.

Bernays, E.A. and Hamai, J. 1987. Head size and shape in relation to gross feeding in Acridoidea (Orthoptera). *Int. J. Insect Morphol.*, 16: 323-338.

Bernhardt, P. and Thien, L.B. 1987. Self-isolation and insect pollination in the primitive angiosperms: new evaluations of older hypotheses. *Plant Syst. Evol.*, 156: 159-176.

Bertin, L. 1923. L'adaptation des pieces buccales aux regimes alimentaires chez les coleopteres lamellicornes. *Ann. Soc. Linn. Lyon*, 69: 145-159.

Bertin, R.I. 1989. Pollination biology. IN: Abrahamson, W.G., (Ed.), *Plant-Animal Interactions*, pp. 23-86. New York: McGraw-Hill Book Company.

Besuchet, C. 1956. Larves et nymphes de pselaphides (Coleoptérès). *Rev. Suisse Zool.*, **63**: 698-705.

Besuchet, C. 1972. Les coleoptérès aculagnathides. *Rev Suisse Zool.*, **79**: 99-145.

Beutel, R. 1986a. Skelet und Muskulatur des Kopfes und Thorax von *Hygrobia tarda* (Herbst). Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Hydradephaga (Insecta: Coleoptera). *Stutt. Beit. Naturk.*, (A), **388**: 1-54.

Beutel, R. 1986b. Skelet und Muskulatur des Kopfes der Larve von *Haliplus lineatocollis* Mrsh. (Coleoptera: Haliplidae). *Stutt. Beitr. Naturk.*, (A), **390**: 1-15.

Beutel, R.G. and Roughley, R.E. 1987. On the systematic position of the genus *Notomicrus* Sharp (Hydadephaga, Coleoptera). *Can. J. Zool.*, **65**: 1898-1905.

Bickel, D.J. 1982. Diptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 563-599. New York: McGraw-Hill.

Bierbrodt, E. 1943. Der Larvenkopf von *Panorpa communis* L. und seine Verwandlung, mit besonderer Berucksichtigung des Gehirns und der Augen. *Zool. Jb. (Anat.)*, **68**: 49-136.

Bigelow, R.S. 1954. Morphology of the face in the Hymenoptera. *Can. J. Zool.*, **32**: 378-392.

Bird, R.D. 1926. The external anatomy of the adult of *Hoplocampa* Nort. (Hym., Tenthred.). *Ann. Entomol. Soc. Am.*, **19**: 268-277.

Bird, R.D. 1927. The external anatomy of the larva of *Hoplocampa halcyon* Nort. with a key to the instars and to those of related species (Tenthredinidae, Hymenoptera). *Ann. Entomol. Soc. Am.*, **20**: 481-486, pl. 24.

Bischoff, W. 1915. Bernstein hymenopteren. *Schrift. Physik.-Okon. Ges. Koningsberg*, **56**: 139-144.

Bischoff, W. 1922a. Uber die Kopfbildung der Dipterenlarven. (Einleitung und 1. Teil: "Die Kopfe der Oligoneuralarven"). *Arch. Naturges.*, (A), **88**: 1-51.

Bischoff, W. 1922a. Uber die Deutung der Mundhaken der Cyclorrhaphalarven. *Arch. Naturges.*, (A), **88**: 51-59.

Bischoff, W. 1924. Ueber die Kopfbildung der Dipterenlarven. Teil III. Die Kopfe der Orthorrhapha-Brachycera-Larven. *Arch. Naturges.*, (A), 90: 1-105.

Bischoff, W. 1927. *Biologie der Hymenopteren*. Berlin. 598 pp.

Bitsch, J. 1952. Recherches anatomiques sur le labium des diploures (Insectes Apterygotes). *Publ. Univ. Dijon*, N.S., 9: 5-26.

Bitsch, J. 1956. Considerations anatomiques sur le palpe maxillaire des Machilidae. *Trav. Lab. Zool., Univ. Dijon*, 15: 1-9, figs. 1-3.

Bitsch, J. 1960. Faune des machilides de Cote-d'Or (Ins. Thysanura). *Trav. Lab. Zool., Univ. Dijon*, 37: 1-23, figs. 1-21.

Bitsch, J. 1963. Morphologie cephalique des machilides (Insecta, Thysanura). *Ann Sci. Nat. (Zool.)*, (12), 5: 585-706.

Bitsch, J. 1966. L'evolution des structures cephaliques chez les larves de Coleoptèeres. *Ann. Soc. Entomol. France*, N.S., 11: 255-324.

Blackith, R.E. and Blackith, R.M. 1966. The anatomy and physiology of the morabine grasshoppers. II. External anatomy and comparisons with Pyrgomorphidae, Acrididae and Proscopiidae. *Aust. J. Zool.*, 14: 1035-1071.

Blackwelder, R.E. 1934. The prostheca or mandibular appendage. *Pan-Pac. Entomol.*, 10: 111-113.

Blackwelder, R.E. 1936. Morphology of the coleopterous family Staphylinidae. *Smithson. Misc. Collns.*, 94: 1-102.

Blaney, W.M. and Chapman, R.F. 1970. The functions of the maxillary palps of Acrididae (Orthoptera). *Entomol. Exp. App.*, 13: 363-376.

Blatchley, W.S. 1926. *Heteroptera or True Bugs of Eastern North America or True Bugs of Eastern North America with Especial Reference to the Faunas of Indiana and Florida*. Indianapolis: Nature Publishing Co. 1116 p.

Bletchly, J.D. 1953. The mouth-parts of the yellow dung-fly, *Scopeuma (=Scatophaga) stercoraria* (L.) (Diptera, Cordyluridae). *Proc. Zool. Soc. London*, 123: 143-165.

Bletchly, J.D. 1954. The mouth-parts of the dance fly, *Empis livida* L. (Diptera, Empididae). *Proc. Zool. Soc. London*, 124: 317-334.

Bletchly, J.D. 1955. The mouth-parts of the down-looker fly, *Rhagio* (=*Leptis*) *scolopacea* (L.) (Diptera, Rhagionidae). *Proc. Zool. Soc. London*, 125: 779-794.

Blunck, H. 1916. Die Metamorphose des Gelbrands (*Dytiscus marginalis* L.). *Zool. Anz.*, 47: 18-31, 33-42.

Blunck, H. 1918. Die Entwicklung des *Dytiscus marginalis* L. vom Ei bis zur Imago. *Z. Wiss. Zool.*, 117: 1-129.

Bode, A. 1905. Orthoptera und Neuroptera aus dem oberen Lias von Braunschweig. *Jb. Preuss. Geol. Landesanst.*, 25: 218, pls. 6-7.

Bode, A. 1953. Die Insektenfauna des Ostniedersächsischen Oberen Lias. *Palaeontographica*, (A), 103: 1-375, pls. 1-15.

Boesel, M.W. 1937. Family Chironomidae. IN: Carpenter, F.M., et al., "Insects and arachnids from Canadian amber." *Univ. Toronto Stud. Geol. Ser.*, 40: 44-55.

Boettger, C.P. 1958. Die systematische Stellung der Apterygota. *Proc. 10th Int. Congr. Entomol.*, 1: 509-516.

Bohart, R.M. 1943. New species of *Halictophagus* with a key to the genus in North America (Strepsiptera, Halictophagidae). *Ann. Entomol. Soc. Am.*, 36: 341-359.

Bohart, R.M. 1946a. A new species of *Halictophagus* parasitic on Cercopidae (Strepsiptera, Halictophagidae). *Proc. Entomol. Soc. Washington*, 48: 200-202.

Bohart, R.M. 1946b. A revision of the Strepsiptera with special reference to the species of North America. *Univ. California Publ. Entomol.*, 7: 91-156, pl. 3.

Bohart, R.M. 1962. A new strepsipteran parasitic on Coreidae. *Proc. Entomol. Soc. Washington*, 64: 91-94.

Bohart, R.M. and Menke, A.S. 1976. *Sphecid Wasps of the World: Generic Revision*. Berkeley: Univ. California Press. 695 p.

Bolender, H. and Homomichl, K. 1985. Ultrastructure of a muscle spindle-analogous receptor organ in the mandible of *Oncopeltus fasciatus* (Insecta, Heteroptera) with remarks on the homology of the mandibular muscles. *Zoomorphologie*, 105: 388-394.

Bonhag, P.F. 1951. The skeleto-muscular mechanism of the head and abdomen of the adult horsefly (Diptera: Tabanidae). *Trans. Am. Entomol. Soc.*, 77: 131-202.

Boomsma, J.J. 1984. Evolutionary aspects of larval food-plant exploitation in Microlepidoptera: an ecological approach to phylogenetic data. *Abstr. 17th Int.Congr. Entomol.*, p. 33.

Boppre, M., Seibt, U. and Wickler, W. 1984. Pharmacophagy in grasshoppers. *Entomol. Exp. Appl.*, 35: 115-117.

Bordas, M.L. 1909. Les glandes cephaliques (glandes sericigenes et glandes mandibulaires) des chenilles de Lepidopteres. *Ann. Sci. Nat. Zool.*, 10: 125-198.

Borden, A.D. 1915. The mouthparts of the Thysanoptera and the relation of thrips to the non-setting of certain fruits and seeds. *J. Econ. Entomol.*, 8: 353-360.

Borkent, A. and Wood, D.M. 1986. The first and second larval instars and the egg of *Parasimulium stonei* Peterson (Diptera: Simuliidae). *Proc. Entomol. Soc. Washington*, 88: 287-296.

Borner, C. 1909. Neue Homologien zwischen Crustaceen und Hexapoden. Die Beissmandibel der Insekten und ihre phylogenetische Bedeutung. Archi- und Metapterygota. *Zool. Anz.*, 34: 100-125.

Borner, C. 1929. Mandibeln und Maxillen bei Psociden, Thysanopteren und Rhynchoten. *Z. Wiss. Insektenbiol.*, 24: 108-116.

Bornman, C.H. and Botha, C.E.J. 1973. The role of aphids in phloem research. *Endeavour*, 32: 129-132.

Borror, D.J., DeLong, D.M. and Triplehorn, C.A. 1976. *An Introduction to the Study of Insects*, 4th edn. New York: Holt, Rinehart and Winston. 852 p.

Botosaneanu, L. 1956a. Recherches sur les Trichoptères de Bulgarie recueillis par MM. le Prof. A Valkanov et B. Rusev. *Beit. Entomol.*, 6: 354-402.

Botosaneanu, L. 1956b. Contributions à la connaissance des stades aquatiques des Trichoptères crénobiontes: *Rhyacophila laevis* Pict., *Wormaldia triangulifera* MacLachl., *Drusus romanicus* Murg. & Bots., *Silovaripilosa* Bots. (Trichoptera). *Beitr. Entomol.*, 6: 590-624.

Botosaneanu, L. and Wichard, W. 1983. Upper-Cretaceous Siberian and Canadian amber caddisflies (Insecta: Trichoptera). *Bijdr. Dierk.*, 53: 187-217.

Botosaneanu, L. and Wichard, W. 1984. Upper-Cretaceous amber Trichoptera. *Proc. Fourth Int. Symp. Trichoptera*, pp. 43-48.

Boucek, Z. 1974. A revision of the Leucospidae (Hymenoptera: Chalcidoidea) of the world. *Bull. Brit. Mus. Nat. Hist. (Entomol.), Suppl.*, 23: 1-241.

Boudreaux, H.B. 1987. *Arthropod Phylogeny with Special Reference to Insects*, rev. edn. Malabar, Florida: Robert E. Krieger. 320 p.

Bourgoin, T. 1986a. Valeur morphologique de la lame maxillaire chez les Hemiptera; remarques phylogenetiques. *Ann. Soc. Entomol. France*, 22: 413-422.

Bourgoin, T. 1986b. Morphologie imaginale du tentorium des Hemiptera Fulgoromorpha. *Int. J. Insect Morphol. Embryol.*, 15: 237-252.

Böving, A.G. 1927a. Immature stages of *Eumycterus sacchardis* (?) Barber, with comments on the classification of the Tribe Barini (Coleoptera: Curculionidae). *Proc. Entomol. Soc. Washington*, 29: 151-158.

Böving, A.G. 1927b. On the classification of the Mylabridae larvae (Coleoptera: Mylabridae). *Proc. Entomol. Soc. Washington*, 29: 133-142, pl. 8.

Böving, A.G. and Craighead, F.C. 1931. *An Illustrated Synopsis of the Principal Larval Forms of the Order Coleoptera*. New York: Brooklyn Entomological Society. 351 p.

Boys, H.A. 1978. Food selection by *Oedaleus senegalensis* (Acrididae: Orthoptera) in grassland and millet fields. *Entomol. Exp. Appl.*, 24: 78-86.

Braack, L.E.O. 1987. Community dynamics of carrion-attendant arthropods in tropical African woodland. *Oecologia*, 72: 402-409.

Brack-Egg, A. 1973. Der Kopf von Rhynchites auratus Scop. (Curculionidae)--Eine konstruktionsmorphologische Untersuchung mit einem Beitrag zum Brutfursorgeverhalten. *Zool. Jb. (Anat.)*, 91: 500-545.

Bradley, J.D., Tremewan, W.G. and Smith, A. 1973. *British Tortricoid Moths. Cochylidae and Tortricidae: Tortricinae*. London: E.W. Classey. 251 p.

Braimah, S.A. 1987a. Mechanisms of filter feeding in immature *Simulium vittatum* Malloch (Diptera: Simuliidae) and *Isonychia campestris* McDunnough (Ephemeroptera: Oligoneuridae). *Can. J. Zool.*, 65: 504-513.

Braimah, S.A. 1987b. Pattern of flow around filter-feeding structures of immature *Simulium bivittatum* Malloch (Diptera: Simuliidae) and *Isonychia campestris* McDunnough (Ephemeroptera: Oligoneuridae). *Can. J. Zool.*, 65: 514-521.

Branch, H. 1913. Morphology and biology of the Membracidae of Kansas. *Kansas Univ. Sci. Bull.*, 8: 75-115, pls. 5-21.

Brauckmann, C. 1988. Hagen-Vorhalle, a new important Namurian Insecta-bearing locality (Upper Carboniferous; FR Germany). *Entomol. Gen.*, 14: 73-79.

Brauckmann, C., Koch, L. and Kemper, M. 1985. Spinnentiere (Arachnida) und Insekten aus den Vorhalle-Schichten (Namurium B; Ober-Karbon) von Hagen-Vorphalle (West-Deutschland). *Geol. Paläont. Westfalen*, 3: 1-131, pls. 1-57.

Brauckmann, C. and Zessin, W. 1989. Neue Meganeuridae aus dem Namurium von Hagen-Vorhalle (BRD) und die Phylogenie der Meganisoptera (Insecta, Odonata). *Deut. Entomol. Z.*, N.F., 36: 177-215.

Brauer, F., Redtenbacher, J. and Ganglbauer, L., 1889. Fosile insekten aus der Juraformation Ost-Sibirens. *Zap. Imp. Akad. Nauk*, (7), 36: 1-22.

Braun, A.F. 1948. Elachistidae of North America. *Mem. Am. Entomol. Soc.*, 13: 1-110, pls. 1-26.

Breckon, G. and Ortiz, V.N. 1983. Pollination of *Zamia pumila* by fungus-gnats. *Am. J. Bot.*, 70: 106-107.

Breitenbach, W. 1882. Beiträge zur Kenntnis des Baues der Schmetterlings-Rüssel. *Jenaische Z. Naturwiss.*, N.S., 15: 151-214, pls. 4-6.

Breithaupt, P.F. 1886. Ueber die Anatomie und die Functionen der Bienenzunge. *Arch. Naturges.*, 52: 47-112, pls. 4-5.

Briant, T.J. 1884. On the anatomy and functions of the tongue of the honey-bee (worker). *J. Linn. Soc.*, 17: 408-417, pls. 18-19.

Briggs, D.E.G., Fortey, R.A. and Clarkson, E.N.K. 1988. Extinction and the fossil record of arthropods. IN: Larwood, G.P., (Ed.), "Extinction and Survival in the Fossil Record." *Syst. Assn. Spec. Vol.*, 34: 171-209.

Brinkhurst, R.O. 1960. Studies on the functional morphology of *Gerris najas* DeGeer (Hem. Het. Gerridae). *Proc. Zool. Soc. London*, 133: 531-559.

Briolini, G. 1960. Ricerche su quattro specie di microlepidotteri miniatori delle fogli di melo. *Nepticula malella* Staint. e *pomella* Vaugh. (Nepticulidae); *Leucoptera scitella* Zell. (Bucculatricidae); *Lithocolletis blancardella* F. (Gracilariidae). *Boll. Ist. Entomol., Bologna Univ.*, 24: 239-269.

Briolini, G. 1965. Ricerche morfologiche ed etologiche su *Paraleucoptera sinuella* Reutti. (Lepidoptera, Lyonetiidae). *Boll. Ist. Entomol., Bologna Univ.*, 27: 229-243.

Britton, E.B. 1960. Beetles from the London Clay (Eocene) of Bognor Regis, Sussex. *Bull. Brit. Mus. Nat. Hist. (Geol.)*, 4: 27-50.

Broadhead, E.C. 1984. Adaptations for fungal grazing in lauxaniid flies. *J. Nat. Hist.*, 18: 639-649.

Broce, A.B. and Elzinga, R.J. 1984. Comparison of prestomal teeth in face fly and house fly (Diptera, Muscidae). *J. Med. Entomol.*, 21: 82-85.

Brocher, F. 1925. L'appareil buccal des larves de *Psylla pyrisuga* Fstr. *Ann. Soc. Entomol. France*, 94: 55-66.

Brodie, P.B. 1845. *A History of the Fossil Insects in the Secondary Rocks of England, Accompanied by a Particular Account of the Strata in which They Occur, and of the Circumstances Connected with Their Preservation*. London: John Van Voorst. 130 pp.

Brongniart, C. 1884. Sur un gigantesque neurorthoptère, provenant des terrains houillers de Commentry. *Comptes Rendus Acad. Sci. France*, 98: 832-833.

Brongniart, C. 1885. Les insectes fossiles des Terrains Primaires. *Bull. Soc. Amis Sci. Nat. Rouen*, 1885: 50-68.

Brongniart, C. 1983. *Insectes Fossiles des Temps Primaires*. Thesis, Saint-Etienne. 493 pp.

Brooks, H.K. 1955. Heal wounds and galls on fossil leaves from the Wilcox deposits (Eocene) of western Tennessee. *Psyche*, 62: 1-9.

Brothers, D.J. 1974. The first Recent species of *Protomutilla* (Hymenoptera: Mutillidae: Myrmosinae). *Psyche*, 81: 268-271.

Brothers, D.J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *Univ. Kansas Sci. Bull.*, 50(11): 483-648.

Brower, L. 1969. Ecological chemistry. *Sci. Am.*, 220: 22-29.

Brown, D.S. 1961. The morphology and functioning of the mouthparts of *Chloeon dipterum* L. and *Baetis rhodani* Pictet (Insecta, Ephemeroptera). *Proc. Zool. Soc. London*, 136: 147-176.

Brown, F.M. 1976. *Oligodonta florissantensis* gen.n., sp. nov. (Lepidoptera: Pieridae). *Bull. Allyn Mus.*, 37: 1-4.

Brown, H.P. 1952. The life history of *Climacea areolaris* (Hagen), a neuropterous "parasite" of fresh water sponges. *Am. Midl. Nat.*, 47: 130-160.

Brown, H.P. and Murvosh, C.M. 1970. *Lutrochus arizonicus* new species, with notes on ecology and behavior (Coleoptera, Dryopoidea, Limnichidae). *Ann. Entomol. Soc. Am.*, 63: 1030-1035.

Brown, V.K. and Hyman, P.S. 1986. Successional communities of plants and phytophagous Coleoptera. *J.Ecol.*, 84: 963-975.

Brown, V.K. and McGavin, G.C. 1982. The biology of some mine and gall forming Diptera on bracken, *Pteridium aqualinum* (L.) Kuhn. *J. Nat. Hist.*, 16: 511-518.

Brown, W.L., Jr. 1969. Ant, paleontology of. *McGraw-Hill Yearbook of Science and Techonology for 1969*, pp. 101-103. New York: McGraw-Hill Publishing Co.

Brown, W.L., Jr. 1982a. Mantodea. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 347-349. New York: McGraw-Hill Book Co.

Brown, W.L., Jr. 1982b. Isoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 349-351. New York: McGraw-Hill Book Co.

Brown, W.L., Jr. 1982c. Gryllolattaria. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 351-352. New York: McGraw-Hill Book Co.

Brown, W.L., Jr. 1982d. Dermaptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 383-386. New York: McGraw-Hill Book Co.

Brown, W.L., Jr. 1982e. Strepsiptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 553-555. New York: McGraw-Hill Book Co.

Brown, W.L., Jr. 1982f. Mecoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 555-557. New York: McGraw-Hill Book Co.

Brown, W.L., Jr. 1982g. Hymenoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 652-680. New York: McGraw-Hill Book Co.

Brown, W.L. and Wilson, E.O. 1959. The evolution of the dacetine ants. *Quart. Rev. Biol.*, 34: 278-294.

Brues, C.T. 1902. Notes on the larvae of some Texan Diptera. *Psyche*, 9: 351-354.

Brues, C.T. 1910. The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. *Bull. Mus. Comp. Zool.*, 54: 1-125.

Brues, C.T. 1920. The selection of food-plants by insects, with special reference to lepidopterous larvae. *Am. Nat.*, 54: 313-332.

Brues, C.T. 1921. Correlation of taxonomic affinities with food habits in Hymenoptera, with special reference to parasitism. *Am. Nat.*, 55: 134-164.

Brues, C.T. 1923. Some new fossil parasitic Hymenoptera from Baltic amber. *Proc. Am. Acad. Arts Sci.*, 58: 327-346.

Brues, C.T. 1924. The specificity of food-plants in the evolution of phytophagous insects. *Am. Nat.*, 58: 127-144.

Brues, C.T. 1926. A species of *Urocerus* from Baltic amber. *Psyche*, 33: 168-170.

Brues, C.T. 1933. The parasitic Hymenoptera of the Baltic amber. *Bernsteinforschungen*, 3: 4-178.

Brues, C.T. 1936. Evidences of insect activity preserved in fossil wood. *J. Paleontol.*, 10: 637-643.

Brues, C.T. 1937. Superfamilies Ichneumonoidea, Serphoidea and Chalcidoidea. IN: Carpenter, F.M., et al., Insects and arachnids from Canadian amber. *Univ. Toronto Stud. Geol. Ser.*, 40: 27-44.

Brues, C.T. 1939. Serphidae in Baltic amber, with description of a new living genus. *Proc. Am. Acad. Sci.*, 73: 259-264.

Brues, C.T. 1972. *Insect Dietary*. Cambridge: Harvard Univ. Press. 466 p.

Brues, C.T., Melander, A.L. and Carpenter, F.M. 1954. Classification of insects: keys to the living and extinct families of insects, and to the living families of other terrestrial arthropods. *Bull. Mus. Comp. Zool.*, 108: 1-917.

Brundin, L. 1976. A Neocomian chironomid and Podonominae-Aphroteniinae (Diptera) in the light of phylogenetics and biogeography. *Zool. Scripta*, 5: 139-160.

Bucher, G.E. 1948, The anatomy of *Monodontomerus dentipes* Boh., an entomophagous chalcid. *Can. J. Res.*, 26D: 230-281.

Buckup, L. 1959. Der Kopf von *Myrsidea cornicis* (DeGeer) (Mallophaga--Amblycera). *Zool. Jb. (Anat.)*, 77: 241-288.

Bugnion, E. 1910. La structure anatomique du *Trigonalys hahni* Spin. *Mitt. Schweiz. Entomol. Ges.*, 12: 14-20, pls. 1-4.

Bugnion, E. 1919. Les organes buccaux de la Scolie. *Mitt. Schweiz. Entomol. Ges.*, 13: 368-396.

Bugnion, E. 1920. Les parties buccales de la blatte et les muscles qui servent a les mouvoir. *Ann. Sci. Nat. (Zool.)* , (10), 3: 41-107.

Bugnion, E. 1927. Les pièces buccales, le sac infrabuccal et le pharynx des fourmis. *Folia Myrmecol. Termitol.*, 1: 27-42.

Bugnion, E. 1929. Les organes bucco-pharynges de deux sphegiens: *Sceliphron (Chalbion) bengalense* Dahlb. et *Sceliphron (Pelopoeus) spirifex* L. *Mitt. Schweiz. Entomol. Ges.*, 14: 139-172.

Bugnion, E. 1930. Les pièces buccales, le sac infrabuccal et le pharynx des fourmis. *Bull. Soc. Roy. Entomol. Egypte*, 40: 85-210.

Bugnion, E. and Popoff, N. 1911. Les pièces buccales des hémiptères (première partie). *Arch. Zool. Exp. Gen.*, (5), 7: 643-674.

Burgess, E. 1878. The anatomy of the head, and the structure of the maxilla in the Psocidae. *Proc. Boston Soc. Nat. Hist.*, 19: 291-296, pl. 8.

Burgess, E. 1880. Contributions to the anatomy of the milk-weed butterfly, *Danais archippus* (Fabr.). *Anniv. Mem. Boston Soc. Nat. Hist.*, 1880: 1-16

Burgess, E. 1881. The structure of the mouth in the larva of *Dytiscus*. *Proc. Boston Soc. Nat. Hist.*, 21: 223-228.

Burks, B.D. 1966. The immature stages of *Axima zabriskiei* Howard (Hymenoptera, Eurytomidae). *Entomol. News*, 77: 199-202.

Burmeister, E.-G. 1976. Der Ovipositor der Hydadephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae. *Zoomorphologie*, 85: 165-257.

Burmeister, H. 1832. *Handbuch der Entomologie*, Volume 1. Berlin: G. Reimer. 698 pp.

Burnham, L. 1978. Survey of social insects on the fossil record. *Psyche*, 85: 85-133.

Burnham, L. 1983. Studies on Upper Carboniferous insects. 1. The Geraridae (Order Protorthoptera). *Psyche*, 90: 1-57.

Burr, M. 1911. Dermaptera (earwigs) perserved in amber from Prussia. *Trans. Linn. Soc. London*, (11), 11: 145-150.

Burtt, E.T. 1940. A filter-feeding mechanism in a larva of the Chironomidae (Diptera: Nematocera). *Proc. Roy. Entomol. Soc. London*, 15: 113-121.

Busck, A. and Boving, A. 1914. On *Mnemonica auricyanea* Walsingham. *Proc. Entomol. Soc. Washington*, 16: 151-162.

Butler, H. 1914. The labium of the Odonata. *Trans. Am. Entomol. Soc.*, 30: 111-134.

Butt, F.H. 1943. Comparative study of mouth parts of representative Hemiptera-Homoptera. *Mem. Cornell Univ. Agr. Exp. Stat.*, 254: 1-20.

Butt, F.H. 1951. Feeding habits and mechanism of the Mexican bean beetle. *Mem. Cornell Univ. Agr. Exp. Stat.*, 306: 1-32.

Butt, F.H. 1957. The role of the premandibular or intercalary segment in head segmentation of insects and other arthropods. *Trans. Am. Entomol. Soc.*, 83: 3-30.

Butt, F.H. 1960. Head development in the arthropods. *Biol. Rev.*, 35: 43-91.

Buttiker, W. 1962. Biological and morphological notes on the fruit-piercing and eye-frequenting moths. *Eleventh Int. Congr. Entomol.*, 2: 10-15, pls. 1, 2.

Buxton, P.A. 1955. *The Natural History of Tsetse Flies*. London: H.K. Lewis and Co. 816 p. + 46 pls.

Byers, G.W. 1973. Zoogeography of the Meropeidae (Mecoptera). *J. Kansas Entomol. Soc.*, 46: 511-516.

Byers, G.W. 1983. *Bittacus banksi* (bitacido, bittacid, hangingfly). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, p. 693. Chicago: University of Chicago Press.

Byers, G.W. 1984. Tipulidae. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 491-514. Dubuque: Kendall/Hunt Publ. Co.

Caillère, L. 1972. Dynamics of the strike in *Agrion* (Syn. *Calopteryx*) *splendens* Harris 1782 larvae (Odonata: Calopterygidae). *Odonatologica*, 1: 11-19.

Caltagirone, L.E. 1984. Adaptations of insects to modes of life. IN: Huffaker, C.B. and Rabb, R.L., (Eds.), *Ecological Entomology*, pp. 217-245. New York: John Wiley and Sons.

Cameron, A.E. 1913. On the life-history of *Lonchaea chorea*, Fabricius. *Trans. Entomol. Soc. London*, **1913**: 314-322, pl. 11.

Cameron, A.E. 1932. The nasal bot fly, *Cephenomyia auribarbis* Meigen (Diptera, Tachinidae) of the red deer, *Cervus elaphus* L. *Parasitology*, 24: 185-195.

Cameron, E. 1958. On the parasites and predators of the cockroach. II. *Evania appendigaster* (L.). *Bull. Entomol. Res.*, 48: 199-209.

Campau, E.J. 1940. The morphology of *Chauliognathus pennsylvanicus* (DeGeer) (Coleoptera: Canthariidae). *Microentomology*, 5: 57-90.

Carayon, J. 1974. Etude sur les hémiptères Plokiophilidae. *Ann. Soc. Entomol. France*, N.S., 10: 499-525.

Carbonell, C.S. 1959. The external anatomy of the South American semi-aquatic grasshopper *Marellia remipes* Uvarov (Acridoidea, Pauliniidae). *Smithson. Misc. Collns.*, **137**: 61-97.

Carne, P.B. 1957. *A Systematic Revision of the Australian Dystinae (Coleoptera: Scarabaeidae)*. Melbourne: Commonwealth Scientific and Industrial Research Organization. 284 p.

Carpenter, F.M. 1929. A Jurassic neuropteran from the lithographic limestone of Bavaria. *Psyche*, 36: 190-194.

Carpenter, F.M. 1930a. The fossil ants of North America. *Bull. Mus. Comp. Zool.*, 70: 1-68, pls. 1-11.

Carpenter, F.M. 1930b. The Lower Permian insects of Kansas. Part 1. Introduction and the order Mecoptera. *Bull. Mus. Comp. Zool.*, 70: 69-101.

Carpenter, F.M. 1931. The biology of the Mecoptera. *Psyche*, 38: 41-55.

Carpenter, F.M. 1932a. The Lower Permian insects of Kansas. Part 5. Psocoptera and additions to the Homoptera. *Am. J. Sci.*, (5), 24: 1-22.

Carpenter, F.M. 1932b. Jurassic insects from Solenhofen in the Carnegie Museum and Museum of Comparative Zoology. *Ann. Carnegie Mus.*, 21: 97-129.

Carpenter, F.M. 1933. The Lower Permian insects of Kansas. Part 6. Delopteridae, Protelytroptera, Plecoptera and a new collection of Protodonata, Odonata, Megasecoptera, Homoptera, and Psocoptera. *Proc. Am. Acad. Arts Sci.*, 68: 409-503.

Carpenter, F.M. 1938. Structure of Permian Homoptera and Psocoptera. *Nature*, 141: 164-165.

Carpenter, F.M. 1939. The Lower Permian insects of Kansas. Part 8. Additional Megasecoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelytroptera, Plectoptera, and Protoperlaria. *Proc. Am. Acad. Arts Sci.*, 73: 29-70.

Carpenter, F.M. 1943a. Carboniferous insects from the vicinity of Mazon Creek, Illinois. *Sci. Pap. Ill. State Mus.*, 3: 9-20.

Carpenter, F.M. 1943b. Osmylidae of the Florissant shales, Colorado (Insecta-Neuroptera). *Am. J. Sci.*, 241: 753-760.

Carpenter, F.M. 1947. Early insect life. *Psyche*, 54: 65-85.

Carpenter, F.M. 1954a. Part III. Extinct families of insects. IN: Brues, C.T., Melander, A.T. and Carptenter, F.M., "Classification of Insects." *Bull. Mus. Comp. Zool.*, 108: 777-827.

Carpenter, F.M. 1954b. The Baltic amber Mecoptera. *Psyche*, 61: 31-40.

Carpenter, F.M. 1956. The Baltic amber snake-flies (Neuroptera). *Psyche*, 63: 77-81.

Carpenter, F.M. 1960a. Fossil Nemopteridae (Neuroptera). *Psyche*, 66: 20-24.

Carpenter, F.M. 1960b. Studies on North American Carboniferous insects. 1. The Protodonata. *Psyche*, 67: 98-110.

Carpenter, F.M. 1963. Studies on Carboniferous insects from Commentry, France. Part 4. The genus *Triplosoba*. *Psyche*, 70: 120-128.

Carpenter, F.M. 1967. Cretaceous insects from Labrador. 2. A new family of snakeflies (Neuroptera: Alloraphidiidae). *Psyche*, 74: 270-275.

Carpenter, F.M. 1971. Adaptations among Paleozoic insects. *Proc. North Am. Paleont. Conv.*, 1: 1236-1251.

Carpenter, F.M. 1977. Geological history and the evolution of the insects. *Proc. 15th Int. Congr. Entomol.*, pp. 63-70.

Carpenter, F.M. and Burnham, L. 1985. The geological record of insects. *Ann. Rev. Earth Planet. Sci.*, 13: 297-314.

Carpenter, F.M., Folsom, J.W., Essig, E.O., Kinsey, A.C., Brues, C.T., Boesel, M.W. and Ewing, H.E. 1934. Insects and arachnids from Canadian amber. *Univ. Toronto Stud. Geol. Ser.*, 40: 7-62.

Carpenter, F.M., Snyder, T.E., Alexander, C.P., James, M.T. and Hull, F.M. 1938. Fossil insects from the Creede Formation, Colorado. Part 1. Introduction, Neuroptera, Isoptera and Diptera. *Psyche*, 45: 105-119.

Carpenter, G.H. and MacDowell, M.C. 1912. The mouth-parts of some beetle larvae (Dascillidae and Scarabaeidae), with especial reference to the maxillulae and hypopharynx. *Quart. J. Micros. Soc.*, 57: 373-396.

Carriker, M.A. 1937. Studies in Neotropical Mallophaga, Part I--lice of the tinamous. *Proc. Acad. Nat. Sci. Philadelphia*, 88: 45-218.

Carroll, C.R. and Janzen, D.H. 1973. Ecology of foraging by ants. *Ann. Rev. Ecol. Syst.*, 4: 231-257.

Carroll, R.L. 1988. *Vertebrate Paleontology and Evolution*. New York: W.H. Freeman and Company. 698 pp.

Carter, D.J. and Dugdale, J.S. 1982. Notes on collecting and rearing *Micropteryx* (Lepidoptera: Micropterigidae) larvae in England. *Entomol. Gaz.*, 33: 43-47.

Carter, W. 1962. *Insects in Relation to Plant Disease*. New York: Interscience. 705 pp.

Center, T.D. and Johnson, C.D. 1974. Coevolution of some seed beetles (Coleoptera: Bruchidae) and their hosts. *Ecology*, 55: 1096-1103.

Chamberlin, J.C. 1923. A revision of the genus *Anisembia*, with description of a new species from the Gulf of California. *Proc. California Acad. Sci.*, (4), 12: 341-351.

Chamberlin, W.J. 1939. *The Bark and Timber Beetles of North America North of Mexico*. Corvallis, Oregon: Oregon State College Assn. 513 p.

Chance, M.M. 1970. The functional morphology of the mouth-parts of blackfly larvae (Diptera: Simuliidae). *Quaest. Entomol.*, **6**: 245-284.

Chao, H.-F. 1953. The external morphology of the dragonfly *Onychogomphus ardens* Needham. *Smithson. Misc. Collns.*, **122**: 1-56.

Chapman, R.F. 1964. The structure and wear of the mandibles in some African grasshoppers. *Proc. Zool. Soc. London*, **142**: 107-121.

Chapman, R.F. 1966. The mouthparts of *Xenocheila zarundnyi* (Ortho ptera, Acrididae). *J. Zool.*, **148**: 277-288.

Chapman, R.F. 1976. A biology of locusts. *Inst. Biol., Stud. Biol.*, **71**: 1-67.

Chapman, R.F. 1982. *The Insects: Structure and Function*, 3rd edn. Cambridge, MA: Harvard University Press. 919 pp.

Chapman, R.F. and Thomas, J.G. 1978. The numbers and distribution of sensilla on the mouthparts of Acridoidea. *Acrida*, **7**: 115-148.

Charnov, E.L. 1976. Optimal foraging: attack strategy of a mantid. *Am. Nat.*, **110**: 141-151.

Chassagnard, M.-T. and Tsacas, L. 1974. Morphologie de la tête et des pieces buccales imaginales de *Chrysopilus auratus* F. et de *Vermileo vermileo* DeG. (Diptera: Rhagionidae). *Int. J. Insect Morphol. Embryol.*, **3**: 13-32.

Chatterjee, N.C. 1933. The life-history and morphology of *Eubrachys tomentosa* Fabr. (Fulgoroidea, Homoptera). *Indian For. Rec., Entomol.*, **18**: 1-26.

Chatterjee, P.N. 1943. Description of *Rhogas plecopterae* sp. nov. from India with notes on its biology and morphology. *Indian J. Entomol.*, **5**: 213-221.

Chaudonneret, J. 1948. Le labium des Thysanoures (Insectes Aptérygotes). *Ann. Sci. Nat., Zool.*, (11), **10**: 1-27.

Chaudonneret, J. 1950. La morphologie cephalique de *Thermobia domestica* (Packard) (Insecte, Apterygote, Thysanoure). *Ann. Sci. Nat. Zool.*, (11), **12**: 145-302.

Chaudonneret, J. 1951. Réflexions sur les prémandibules des larves de Culicides (Diptères Nématocères). *Bull. Soc. Zool. France*, **76**: 399-404.

Chaudonneret, J. 1958. A propos de l'origine embryonnaire du crâne des insectes. II. Quelques réflexions sur la notion métamère. *Bull. Soc. Zool. France*, 83: 413-422.

Chaudonneret, J. 1962. Quelques dispositifs remarquables dans les organes de l'ingestion chez la larve de moustique (Diptera, Nematocera). *Ann. Sci. Nat., Zool.*, (12), 4: 473-487.

Chaudonneret, J. 1963. Le problème des "messores" des larves de Diptères Nématocères et la musculature labrale des insectes. *Bull. Soc. Zool. France*, 88: 369-378.

Chaudonneret, J. 1965. Le clypeo-labre et la barre cibariale chez la larve de Culex (Diptere Nématocère). Leur signifation morphologique. *Ann. Sci. Nat., Zool.*, 7: 743-766.

Chaudonneret, J. 1982. Les pièces buccales des insectes: th'me et variations. I. *Bull. Sci. Bourgonge*, 35: 65-86.

Chaudonneret, J. 1983. Les pièces buccales des insectes: thème et variations. II. *Bull. Sci. Bourgonge*, 36: 116-133.

Chaudonneret, J. 1984a. Les pièces buccales des insectes: thème et variations. III. *Bull. Sci. Bourgonge*, 37: 11-26.

Chaudonneret, J. 1984b. Les pièces buccales des insectes: thème et variations. IV. *Bull. Sci. Bourgonge*, 37: 86-94.

Chaudonneret, J. 1986. Les pièces buccales des insectes: thème et variations. V. *Bull. Sci. Bourgonge*, 39: 26-45.

Chaudonneret, J. 1987. Les pièces buccales des insectes: thème et variations. VI. *Bull. Sci. Bourgonge*, 40: 25-52.

Chaudonneret, J. 1989a. Les pièces buccales des insectes: thème et variations. VII. *Bull. Sci. Bourgonge*, 42: 8-45.

Chaudonneret, J. 1989b. Les pièces buccales des insectes: thème et variations. VIII. *Bull. Sci. Bourgonge*, 42: 87-143.

Chauvin, G. and Faucheux, M. 1981. Les pièces buccales et leurs recepteurs sensoriels chez l'imago de *Micropteryx calthella* L. (Lepidoptera: Micropterygidae). *Int. J. Insect Morphol. Embryol.*, 10: 425-439.

Cheng, L. 1976. Insects in marine environments. IN: Cheng, L., (Ed.), *Marine Insects*, pp. 1-4. New York: North-Holland Publ. Co.

Chernova, O.A. 1961. The taxonomic position and geological age of mayflies of the genus *Ephemeropsis* Eichwald (Ephemeroptera, Hexagenitidae). *Entomol. Rev.*, **40**: 485-493.

Chernova, O.A. 1965. Some fossil mayflies (Ephemeroptera, Misthodotidae) from Permian beds of the Ural. *Entomol. Rev.*, **44**: 202-207.

Chernova, O.A. 1967. Mayflies of a Recent family in the Jurassic of Transbaikalia (Ephemeroptera, Siphlonuridae). *Entomol. Rev.*, **46**: 193-196.

Chernova, O.A. 1968. New mayflies from Karatau (Ephemeroptera). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 7-22. Moscow: Academy of Sciences. [In Russian.]

Chernova, O.A. 1970. On the classification of fossil and recent Ephemeroptera. *Entomol. Rev.*, **49**: 71-81.

Chernova, O.A. 1971. A mayfly (Ephemeroptera, Leptophlebiidae) from fossil resin of Cretaceous deposits in the polar regions of Siberia. *Entomol. Rev.*, **50**: 346-349.

Chernova, O.A. 1977. Distinctive new mayfly nymphs (Emphemeroptera: Palingeniidae, Behningiidae) from the Jurassic of Transbaikalia. *Paleontol. J.*, **1977**: 221-226.

Chernova, O.A. 1980. Order Ephemerida. IN: Rohdendorf, B.B. and Rasnitsyn, A.G., (Eds.), "Historical Development of the Class Insecta." *Trans. Paleontol. Inst.*, **175**: 31-36.

Chessman, B.C. 1986. Dietary studies of aquatic insects from two Victorian rivers. *Aust. J. Freshw. Res.*, **37**: 129-146.

Chillcott, J.G. 1960. A revision of the Nearctic species of Fanniinae (Diptera: Muscidae). *Can. Entomol. Suppl.*, **14**: 1-295.

China, W.E. 1931. Morphological parallelism in the structure of the labium in the hemipterous genera *Coptosomoides*, gen. nov., and Bozius, Dist. (Fam Plataspidae) in connection with mycetophagous habits. *Ann. Mag. Nat. Hist.*, (10), **7**: 281-286.

China, W.E. 1933. A new family of Hemiptera-Heteroptera, with notes on the phylogeny of the suborder. *Ann. Mag. Nat. Hist.*, (10). **12**: 180-196.

China, W.E. 1935. New and little-known Helotrephidae. *Ann. Mag. Nat. Hist.*, (10), **15**: 593-614.

China, W.E. 1936. The first genus and species of Helotrephidae (Hemiptera) from the New World. *Ann. Mag. Nat. Hist.*, (10), 17: 527-538.

China, W.E. 1945. A completely blind bug of the family Lygaeidae (Hemiptera Heteroptera). *Proc. Roy. Soc. London*, (B), 14: 126-128.

China, W.E. 1955. A reconsideration of the systematic position of the family Joppeicidae Reuter (Hemiptera-Heteroptera), with notes on the phylogeny of the suborder. *Ann. Mag. Nat. Hist.*, (12), 8: 353-370.

China, W.E. 1956. A new species of the genus *Hermatobates* from the Hawaiian Islands (Hemiptera-Heteroptera, Gerridae, Halobatinae). *Ann. Mag. Nat. Hist.*, (12), 9: 353-357.

China, W.E. 1957. The marine Hemiptera of the Monte Bello Islands with descriptions of some allied species. *J. Linn. Soc. London*, 43: 342-357.

China, W.E. and Fennah, R.C. 1952. A remarkable new genus and species of Fulgoroidea (Homoptera) representing a new family. *Ann. Mag. Nat. Hist.*, (12), 5: 189-199.

Chisholm, I.F. and Lewis, T. 1984. A new look at thrips Thysanoptera) mouthparts, their action and effects of feeding on plant tissue. *Bull. Entomol. Res.*, 74: 663-675.

Chisholm, P.J. 1962. The anatomy in relation to feeding habits of *Perla cephalotes* Curtis (Plecoptera, Perlidae) and other Plecoptera. *Trans. Soc. Brit. Entomol.*, 15: 55-101.

Chiswell, J.R. 1955. On the last instar larva of *Tipula livida* Van Der Wulp (Diptera, Tipulidae), with notes on the frontoclypeal region of larval Tipulinae and caterpillars. *Proc. Roy. Entomol. Soc. London*, 30A: 127-136.

Chopard, L. 1936. Orthoptères fossiles et subfossiles de l'ambre et du copal. *Ann. Soc. Entomol. France*, 105: 375-386.

Christianson, K. 1964. Bionomics of Collembola. *Ann. Rev. Entomol.*, 9: 147-178.

Christianson, K. 1971. Notes on Miocene amber Collembola from Chiapas. *Univ. California Publ. Entomol.*, 63: 45-48.

Christophers, S.R., Shortt, H.E. and Barraud, P.J. 1926. The anatomy of the sandfly *Phlebotomus argentipes* Ann. and Brun. (Diptera). 1. The head and mouth parts of the imago. *Indian Med. Res. Mem.*, 4: 177-204.

Chrystal, R.N. 1930. Studies of the *Sirex* parasites. The biology and post-embryonic development of *Ibalia leucospoides* Hochenw. (Hymenoptera-Cynipoidea). *Oxford For. Mem.*, 11: 1-63, pls. 1-10.

Chutter, F.M. 1961. Certain aspects of the morphology and ecology of the nymphs of several species of *Pseudagrion* Selys (Odonata). *Arch. Hydrobiol.*, 57: 430-463.

Claassen, P.W. 1931. *Plecoptera Nymphs of America (North of Mexico).* Springfield, IL: Charles Thomas, Publishers. 199 p.

Clairidge, M.F. 1987. Insect assemblages--diversity, organization, and evolution. IN: Gee, J.H.R. and Giller, P.S., (Eds.), *Organization of Communities Past and Present*, pp. 141-162. Oxford: Blackwell Scientific Publications.

Clairville, J.P. de 1798-1806. *Helvetische Entomologie, oder Verzeichniss der Schweizerischen Insekten [Coleoptera]. Nach einer neuen Methode Geordnet. Mit Beschreibungen und Abbildungen.* Erster-[zweiter] Teil.

Clancy, D.W. 1946. The insect parasites of the Chrysopidae Neuroptera). *Univ. California Publ. Entomol.*, 7: 403-496.

Clark, T. 1949. Piercing mouth-parts in the biting lice Mallophaga). *Nature*, 164: 617.

Clarke, J.F.G. 1941. Revision of the North American moths of the Family Oecophoridae, with descriptions of new genera and species. *Proc. U.S. Natl. Mus.*, 90(3107): 33-286, pls. 1-48.

Clausen, C.P. 1923. The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*. *Ann. Entomol. Soc. Am.*, 16: 195-217.

Clausen, C.P. 1940. *Entomophagous Insects*. New York: McGraw-Hill Book Company. 688 p.

Cleveland, L.R. 1934. The wood-feeding roach *Cryptocercus*, its protozoa, and the symbiosis between protozoa and roach. *Mem. Am. Acad. Arts Sci.*. 17: 1-342, pls. 1-60.

Cloudsley-Thompson, J.L. 1988. *Evolution and Adaptation of Terrestrial Arthropods*. Berlin: Springer-Verlag. 141 pp.

Cobben, R.H. 1970. Morphology and taxonomy of intertidal dwarfbugs (Heteroptera: Omaniidae fam. nov.). *Tijdsch. Entomol.*, 113: 61-90.

Cobben, R.H. 1971. A fossil shore bug from the Tertiary amber of Chiapas, Mexico (Heteroptera, Saldidae). *Univ. California Publ. Entomol.*, 63: 49-56.

Cobben, R.H. 1978. Evolutionary trends in Heteroptera. Part II. Mouthpart-structures and feeding strategies. *Meded. Landbouwhoges. Wagen.*, 78-5: 1-407.

Cochereau, P. 1974. Les papillons piqueurs de fruits et leurs commensaux. *Cahier ORSTOM, Ser. Biol.*, 22: 1-42.

Cockerell, T.D.A. 1906a. Fossil Hymenoptera from Florissant, Colorado. *Bull. Mus. Comp. Zool.*, 50: 1-58.

Cockerell, T.D.A. 1906b. Bees of Florissant, Colorado. *Bull. Am. Mus. Nat. Hist.*, 22: 419-455.

Cockerell, T.D.A. 1907a. A fossil butterfly of the genus *Chlorippe*. *Can. Entomol.*, 39: 361-362.

Cockerell, T.D.A. 1907b. A fossil tsetse fly in Colorado. *Nature*, 76: 414.

Cockerell, T.D.A. 1907c. Some Old World types of insects in the Miocene of Colorado. *Science*, 26: 446-447.

Cockerell, T.D.A. 1908. Fossil Osmylidae (Neuroptera) in America. *Can. Entomol.*, 40: 341-342.

Cockerell, T.D.A. 1909a. Fossil Diptera from Florissant, Colorado. *Bull. Am. Mus. Nat. Hist.*, 26: 9-12.

Cockerell, T.D.A. 1909b. Fossil insects from Florissant, Colorado. *Bull. Am. Mus. Nat. Hist.*, 26: 67-76.

Cockerell, T.D.A. 1909c. Another fossil tsetse fly. *Nature*, 80: 128.

Cockerell, T.D.A. 1909d. Descriptions of Tertiary insects. Some new Diptera. *Am. J. Sci.*, (4), 27: 381-387.

Cockerell, T.D.A. 1909e. Descriptions of Hymenoptera from Baltic amber. *Schrift. Physik.-Okon Ges. Koningsberg*, 51: 1-20.

Cockerell, T.D.A. 1910. Fossil insects and a crustacean from Florissant, Colorado. *Bull. Am. Mus. Nat. Hist.*, 28: 275-288.

Cockerell, T.D.A. 1911. Fossil insects from Florissant, Colorado. *Bull. Am. Mus. Nat. Hist.*, 30: 71-82.

Cockerell, T.D.A. 1913a. The first fossil anthomyid fly from Florissant (Dipt.). *Entomol. News*, 24: 295-296.

Cockerell, T.D.A. 1913b. The first mydaid fly. *Entomologist*, 46: 207-208.

Cockerell, T.D.A. 1916a. Insects in Burmese amber. *Am. J. Sci.*, 42: 135-138.

Cockerell, T.D.A. 1916b. British fossil insects. *Proc. U.S. Natl. Mus.*, 49: 469-499, pls. 60-65.

Cockerell, T.D.A. 1917a. Arthropods in Burmese amber. *Psyche*, 24: 40-45.

Cockerell, T.D.A. 1917b. A fossil tsetse fly and other Diptera from Florissant, Colorado. *Proc. Biol. Soc. Washington*, 30: 19-22.

Cockerell, T.D.A. 1919a. Two interesting insects in Burmese amber. *Entomologist*, 52: 193-195.

Cockerell, T.D.A. 1919b. New species of North American fossil beetles, cockroaches and tsetse flies. *Proc. U.S. Natl. Mus.*, 54: 301-311.

Cockerell, T.D.A. 1921. Fossil arthropods in the British Museum. VI. Oligocene insects from Gurnet Bay, Isle of Wight. *Ann. Mag. Nat. Hist.*, (9), 7: 453-480.

Cockerell, T.D.A. 1922. A fossil moth from Florissant, Colorado. *Am. Mus. Novit.*, 34: 1-2.

Cockerell, T.D.A. 1925a. Tertiary insects from Kudia River Maritime Province, Siberia. *Proc. U.S. Natl. Mus.*, 68: 1-16.

Cockerell, T.D.A. 1925b. The Eocene fossil fly *Eophlebomyia*. *Psyche*, 32: 229-230.

Cockerell, T.D.A. 1925c. Fossil insects in the United States National Museum. *Proc. U.S. Natl. Mus.*, 64: 1-15.

Cockerell, T.D.A. 1926. A new fossil moth from Florissant. *Psyche*, 33: 16-17.

Cockerell, T.D.A. 1927. New light on the giant fossil mayflies of Mongolia. *Am. Mus. Novit.*, 244: 1-4.

Coffman, W.P. and Ferrington, L.C., Jr. 1984. Chironomidae. IN: Merritt, R.W. and Cummins, K.W., eds., *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 551-652. Dubuque, IA: Kendall/Hunt Publ. Co.

Cole, F.R. 1969. *The Flies of Western North America*. Berkeley: University of California Press. 693 p.

Colless, D.H. 1962. A new Australian genus and family of Diptera (Nematocera: Perissosomatidae). *Aust. J. Zool.*, 10: 519-535.

Colless, D.H. 1977. A possibly unique feeding mechanism in a dipterous larva (Diptera: Culicidae: Chaoborinae). *J. Aust. Entomol. Soc.*, 16: 335-339.

Common, I.F.B. 1966. A new family of Bombycoidea (Lepidoptera) based on *Carthaea saturnioides* Walker from Western Australia. *J. Aust. Entomol. Soc.*, 5: 29-36.

Common, I.F.B. 1973. A new family of Dacnonympha (Lepidoptera) based on three new species from southern Australia, with notes on the Agathiphagidae. *J. Aust. Entomol. Soc.*, 12: 11-23.

Common, I.F.B. 1975. Evolution and classification of the Lepidoptera. *Ann. Rev. Entomol.*, 20: 183-203.

Common, I.F.B. 1979. The larvae and pupae of *Imma acosma* (Turner) and *I. vaticina* Meyrick (Lepidoptera: Immidae), and the taxonomic relationships of the family. *J. Aust. Entomol. Soc.*, 18: 33-38.

Comstock, J.H. 1977. *An Introduction to Entomology*, 9th edn. Ithaca, N.Y.: Cornell Univ. Press. 1064 p.

Comstock, J.H. and Kochi, C. 1902. The skeleton of the head of insects. *Am. Nat.*, 36: 13-45.

Condal, L.F. 1951. Nuevos hallazgos en el Jurasico Superior del Montsech. *Notas Comun. Inst. Geol. Min. España*, 23: 45-62, pls. 1-10.

Cook, E.F. 1943. The heads of some Coleoptera. *Microentomology*, 8: 25-40.

Cook, E.F. 1944a. The morphology and musculature of the labrum and clypeus of insects. *Microentomology*, 9: 1-35.

Cook, E.F. 1944b. The morphology of the larval heads of some Culicidae (Diptera). *Microentomology*, 9: 38-68.

Cook, E.F. 1944c. On the morphology of the larval head of a species of *Chironomus* (Diptera: Chironomnidae). *Microentomology*, 9: 69-77.

Cook, E.F. 1949. The evolution of the head in the larvae of the Diptera. *Microentomology*, **14**: 1-57

Cook, E.F. 1971. Fossil Scatopsidae in Mexican amber (Diptera: Insecta). *Univ. California Publ. Entomol.*, **63**: 57-61.

Cook, E.F. 1981. Chaoboridae. IN: McAlpine, J.F., et al. (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 335-339.

Cope, J.C.W., et al. 1981. A correlation of Jurassic rocks in the British Isles. Part I. *Spec. Rept. Geol. Soc. London*, 14: 1-73.

Cope, O.B. 1940. The morphology of *Psocus confraternus* Bankson (Psocoptera: Psocidae). *Microentomology*, **5**: 91-115.

Cope, O.B. 1941. The morphology of a species of the genus *Tetrophthalmus* (Mallophaga: Menoponidae). *Microentomology*, **6**: 71-92.

Corbet, P.S. 1951. The development of the labium of *Sympetrum striolatum* (Charp.) (Odon., Libellulidae). *Entomol. Mon. Mag.*, **87**: 289-296.

Corbet, P.S. 1953. A terminology for the labium of larval Odonata. *Entomologist*, **86**: 191-196.

Corbet, S.A. 1971. Mandibular gland secretion of larvae of the flour moth, *Anagasta kuehniella*, contains an epideictic pheromone and elicits oviposition movements in a hymenopteran parasite. *Nature*, **232**: 481-484.

Corbière, G. 1967. Anatomie sensorielle des appendices céphaliques de la larve du Speophyes lucidulus (Delar.) (col'optère cavernicole de la sous-famille des Bathysciinae). *Ann. Spéléol.*, **22**: 417-431.

Costa, C., Casari-Chen, S.A. and Vanin, S.A., 1985. Larvae of Neotropical Coleoptera. XII. Artematopoidea, Artematopidae. *Rev. Bras. Entomol.*, **29**: 309-314.

Costa Cruz, C. 1962. Anatomia e histologia comparádas das glandulas mandibulares dos Meliponideos. *Arquiv. Mus. Nac.*, **52**: 79-84.

Costa Lima, A.M. 1968. *Quarto Catalogo dos Insectos que Vivem nas Plantas do Brasil seus Parasitos e Predatores*. Rio de Janeiro: Ministerio da Agricultura. 2 volumes, 887 p.

Cowen, R. 1979. Morphology, functional. IN: Fairbridge, R.W. and Jablonski, D., (Eds.), *The Encyclopedia of Paleontology*, p. 487-492. Stroudsburg, PA: Dowden, Hutchinson and Ross, Inc.

Cowley, D.R. 1978. Studies on the larvae of New Zealand Trichoptera. *New Zealand J. Zool.*, 5: 639-750.

Cragg, F.W. 1912a. Studies on the mouth parts and sucking apparatus in the blood-sucking Diptera. No. 1. *Philaematomyia insignis*, Austen. *Sci. Mem. Off. Med. Sanit. Depts, Govt. India*, 54: 1-17, pls. 1-5.

Cragg, F.W. 1912b. The structure of *Haematopota pluvialis* (Meigen). *Sci. Mem. Off. Med. Sanit. Depts., Govt. India*, 55: 1-36, pls. 1-7.

Cragg, F.W. 1913a. Studies on the mouth parts and sucking apparatus of the blood-sucking Diptera. No. 2. Some observations on the morphology and mechanism of the parts in the Orthorrapha. *Sci. Mem. Off. Med. Sanit. Depts., Govt. India*, 58: 1-33, pl. 1.

Cragg, F.W. 1913b. Studies on the mouth parts and sucking apparatus of the blood-sucking Diptera. No. 3. *Lyperosia minuta*, Bezzi. *Sci. Mem. Off. Med. Sanit. Depts., Govt. India*, 59: 1-36, pls. 1-6.

Cragg, F.W. 1913c. Studies on the mouth parts and sucking apparatus of the blood-sucking Diptera. No. 4. The comparative anatomy of the proboscis in the blood-sucking Muscidae. *Sci. Mem. Off. Med. Sanit. Depts., Govt. India*, 60: 1-56, pls. 1-5.

Craig, D.A. 1974. The labrum and cephalic fans of larval Simuliidae (Diptera: Nematocera). *Can. J. Zool.*, 52: 133-159, pls. 1-5.

Craig, D.A. 1977a. Mouthparts and feeding behaviour of Tahitian larval Simuliidae (Diptera: Nematocera). *Quaest. Entomol.*, 13: 195-218.

Craig, D.A. 1977b. A re-assessment of the systematic position of *Pseudosimilium humidum* (Westwood), an Upper Jurassic fossil dipteran. *Entomol. Gaz.*, 28: 175-179.

Craig, D.A. and Chance, M.M. 1982. Filter feeding in larvae of Simuliidae (Diptera: Culicomorpha): aspects of functional morphology and hydrodynamics. *Can. J. Zool.*, 60: 712-724.

Crampton, G.C. 1916. A comparative study of the maxillae of the Acridiidae (Oedipodinae and Tettiginae), Phasmidae and Phylliidae. *Psyche*, 23: 83-88.

Crampton, G.C. 1917a. A phylogenetic study of the lateral head, neck and prothoracic regions in some Apterygota and lower Pterygota. *Entomol. News*, 28: 398-412.

Crampton, G.C. 1917b. A phylogenetic study of the larval and adult head in Neuroptera, Mecoptera, Diptera, and Trichoptera. *Ann. Entomol. Soc. Am.*, 10: 337-344.

Crampton, G.C. 1920a. Some anatomical details of the remarkable winged zorapteron, *Zorotypus hubbardi* Caudell, with notes on its relationships. *Proc. Entomol. Soc. Washington*, 22: 98-106.

Crampton 1920b. A comparison of the external anatomy of the lower Lepidoptera and Trichoptera from the standpoint of phylogeny. *Psyche*, 27: 23-34, pls. 2-3.

Crampton, G.C. 1921a. The phylogenetic origin of the mandibles of insects and their arthropodan relatives--a contribution to the study of the evolution of the Arthropoda. *J. New York Entomol. Soc.*, 29: 63-100.

Crampton, G.C. 1921b. The origin and homologies of the so-called "superlingulae" or "paraglossae" (paragnaths) of insects and related arthropods. *Psyche*, 28: 84-92.

Crampton, G.C. 1921c. The sclerites of the head, and the mouth-parts of certain immature and adult insects. *Ann. Entomol. Soc. Am.*, 14: 65-103.

Crampton, G.C. 1923a. A comparison of the labium in certain holometabolous insects from the standpoint of phylogeny. *Proc. Entomol. Soc. Washington*, 25: 171-180.

Crampton 1923b. A phylogenetic comparison of the maxillae throughout the orders of insects. *J. New York Entomol. Soc.*, 31: 77-101, pls. 12-17.

Crampton, G.C. 1925a. A phylogenetic study of the labium of holometabolous insects, with particular reference to the Diptera. *Proc. Entomol. Soc. Washington*, 27: 68-91.

Crampton, G.C. 1925b. The external anatomy of the head and abdomen of the roach, *Periplaneta americana*. *Psyche*, 32: 195-220.

Crampton, G.C. 1926a. The affinities of *Grylloblatta* as indicated by a study of the head and its appendages. *Psyche*, 33: 78-85.

Crampton, G.C. 1926b. The external anatomy of the primitive tanyderid dipteran *Macrochile spectrum* Loew, preserved in Baltic amber. *Bull. Brooklyn Entomol. Soc.*, 21: 1-14.

Crampton, G.C. 1927. *Eugereon* and the ancestry of the Hemiptera, psocids and Hymenoptera. *Bull. Brooklyn Entomol. Soc.*, 22: 1-15.

Crampton, G.C. 1928a. The eulabium, mentum, submentum and gular region of insects. *J. Entomol. Zool.*, 20: 1-13.

Crampton, G.C. 1928b. The evolution of insects, chilopods, diplopods, Crustacea and other arthropods indicated by a study of the head capsule. *Can. Entomol.*, 40: 129-141.

Crampton, G.C. 1930a. The head structures of the orthopteron *Stenopelmatus*--a contribution to the study of the external anatomy of *Stenopelmatus*. *Pan-Pac. Entomol.*, 6: 97-110.

Crampton, G.C. 1930b. A comparison of the more important structural details of the larva of the archaic tanyderid dipteron *Protoplasa fitchii* with other Holometabola from the standpoint of phylogeny. *Bull. Brooklyn Entomol. Soc.*, 25: 239-258.

Crampton, G.C. 1932. A phylogenetic study of the head capsule in certain orthopteroid, psocoid, hemipteroid and holometabolous insects. *Bull. Brooklyn Entomol Soc.*, 27: 19-50.

Crampton, G.C. 1942. The external morphology of the Diptera. *Bull. Conn. Geol. Nat. Hist. Surv.*, 64: 10-165.

Crane, P.R. and Jarzembowski, E.A. 1980. Insect leaf mines from the Palaeocene of southern England. *J. Nat. Hist.*, 14: 620-636.

Cranston, F.P. and Sprague, I.B. 1961. A morphological study of the head capsule of *Gerris remigis* Say. *J. Morphol.*, 108: 287-309.

Cregan, M.B. 1941. Generic relationships of the Dolichopodidae (Diptera) based on a study of the mouth parts. *Ill. Biol. Mon.*, 18: 1-68.

Crepet, W.L. 1972. Investigations of North American cycadeoids: pollination mechanisms in Cycadeoidea. *Am. J. Bot.*, 59: 1048-1056.

Crepet, W.L. 1974. Investigations of North American cycadeoids: the reproductive biology of Cycadeoidea. *Palaeontographica*, (B), 148: 144-169, pls. 52-72.

Crepet, W.L. 1979a. Insect pollination: a palaeontological perspective. *Bioscience*, 29: 102-108.

Crepet, W.L. 1979b. Some aspects of the pollination biology of Middle Eocene angiosperms. *Rev. Palaeobot. Palynol.*, 27: 213-238.

Crepet, W.L. 1983. The role of insect pollination in the evolution of the angiosperms. IN: Real, L., (Ed.), *Pollination Biology*, pp. 29-50. New York: Academic Press.

Crepet, W.L. 1984. Advanced (constant) insect pollination mechanisms: pattern of evolution and implications vis-a-vis angiosperm diversity. *Ann. Missouri Bot. Gard.*, 71: 607-630.

Crepet, W.L. and Friis, E.M. 1987. The evolution of insect pollination in angiosperms. IN: Friis, E.M., Chaloner, W.G. and Crane, P.R., (Eds.), *The Origins of Angiosperms and Their Biological Consequences*, pp. 181-201. New York: Cambridge University Press.

Crepet, W.L. and Taylor, D.W. 1985. The diversification of the Leguminosae: first fossil evidence of the Mimosoideae and Papilionoideae. *Science*, **228**: 1087-1089.

Cresson, E.T. 1887. Synopsis of the families and genera of the Hymenoptera of America, north of Mexico, together with a catalogue of the described species, and bibliography. *Trans. Am. Entomol. Soc., Suppl.*, **1887**: 1-351.

Crichton, M.E. 1957. The structure and function of the mouth parts of adult caddis flies (Trichoptera). *Phil. Trans. Roy. Soc. London*, **241**: 45-91.

Crome, W. 1957. Zur Morphologie und Anatomie der Larve von *Oryctes nasicornis* L. *Deut. Entomol. Z.*, N.S., **4**: 228-262.

Crosskey, R.W. 1951. The morphology, taxonomy, and biology of the British Evanioidea (Hymenoptera). *Trans. Roy. Entomol. Soc. London*, **102**: 247-281.

Crouzel, I.S. and Salavin, R.G. 1943. Contribucion al estudio de los *Neorhynchocephalus argentinos* (Diptera: Nemestrinidae). *An. Soc. Cien. Argentina*, **136**: 145-177.

Crowson, R.A. 1955. *The Natural Classification of the Families of Coleoptera*. London: Nathaniel Lloyd.

Crowson, R.A. 1959. Studies on the Dermestoidea (Coleoptera), with special reference to the New Zealand fauna. *Trans. Roy. Entomol. Soc. London*, **111**: 81-94.

Crowson, R.A. 1964. A new genus of Australian clavicorn Coleoptera, probably of a new family. *Proc. Linn. Soc. New South Wales*, **89**: 241-245.

Crowson, R.A. 1967. *The Natural Classification of the Families of Coleoptera*. Middlesex, Great Britain: E.W. Classey, Ltd.

Crowson, R.A. 1972. A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families, Cneoglossidae and Omethidae. *Rev. Univ. Madrid*, **21**: 35-77.

Crowson, R.A. 1973. Further observations on Phloeostichidae and Cavognathidae, with definitions of new genera from Australia and New Zealand. *Coleopt. Bull.*, **27**: 54-62.

Crowson, R.A. 1976. The evolutionary history of Coleoptera, as documented by fossil and comparative evidence. *Atti 10th Congr. Naz. Ital. Entomol.*, pp. 47-90.

Crowson, R.A. 1981. *The Biology of the Coleoptera.* New York: Academic Press. 802 p.

Crowson, R.A. 1985. Comments on Insecta of the Rhynie Chert. *Entomol. Gen.*, 11: 97-98.

Crowson, R.A., Rolfe, W.D.I., Smart, J., Waterston, C.D., Willey, E.C. and Wootton, R.J. 1967. Arthropoda: Chelicerata, Pycnogonida, *Palaeoisopus*, Myriapoda and Insecta. IN: Harland, W.B., et al., (Eds.), *The Fossil Record*, pp. 499-534. London: Geological Society of London.

Crowson, R.A. and Sen Gupta, T., 1969. The systematic position of Propalcticidae and of *Carinophloeus* Lefkovitch (Coleoptera, Clavicornia) with description of a new species of *Propalticus* and of its supposed larva. *Proc. Roy. Entomol. Soc. London*, (B), 38: 132-140.

Crowson, R.A. and Viedma, M.G. de, 1964. Observations on the relationships of the genera *Circaeus* Yablok. and *Mycterus* Clairv. with a description of the presumed larva of *Mycterus* (Col. Heteromera). *Eos*, 40: 99-107.

Cruden, R.W., Hermann, S.M. and Peterson, S. 1983. Patterns of nectar production and plant-pollinator coevolution. IN: Bently, B. and Elias, T., (Eds.), *The Biology of Nectaries*, pp. 80-125. New York: Columbia University Press.

Crumb, S.E. 1956. The larvae of the Phalaenidae. *U.S. Dept. Agr. Tech. Bull.*, 1135: 1-356, pls. 1-10.

Cuffey, R.J, Kim, K.C., Smith, D.K. and Thornton, C.P. 1982. Latest Oligocene insects from the Creede Caldera in southwestern Colorado. *Proc. 3rd No. Am. Paleontol. Conv.*, 1: 119-123.

Cummings, B.F. 1912. On some points in the anatomy of the mouth-parts of the Mallophaga. *Proc. Zool. Soc. London*, 1913: 128-141.

Cummings, B.F. 1913. Apropos of the first maxillae in the genus *Dipseudopsis*, Walk., Trichoptera. *Ann. Mag. Nat. Hist.*, (8), 11: 308-312.

Cummings, B.F. 1914a. Note on the characters of the head and mouthparts in the genera *Plectrotarsus* and *Aethaloptera* (Trichoptera). *Ann. Mag. Nat. Hist.*, (8), 14: 22-31.

Cummings, B.F. 1914b. Scent organs in Trichoptera. *Proc. Zool. Soc. London*, 1914: 459-474.

Cummins, K.W. 1973. Trophic relations of aquatic insects. *Ann. Rev. Entomol.*, 18: 183-206.

Cummins, K.W. and Klug, M.J. 1979. Feeding ecology of stream invertebrates. *Ann. Rev. Ecol. Syst.*, 10: 147-172.

Cummins, K.W. and Merritt, R.W. 1984. General morphology of aquatic insects. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 4-10. Dubuque: Kendall/Hunt Publ. Co.

Curran, C.H. 1965. *The Families and Genera of North American Diptera*, 2nd rev. edn. Woodhaven, New York: Henry Tripp. 515 p.

Currie, G.A. 1937. Galls on *Eucalyptus* trees: a new type of association between flies and nematodes. *Proc. Linn. Soc. New South Wales*, 62: 147-174.

Cutler, J.R. 1955. The morphology of the head of the final instar larva of *Nasonia vitripennis* Walker (Hymenoptera: Chalcidoidea). *Proc. Roy. Entomol. Soc. London*, (A), 30: 73-81.

Dahl, C., Widahl, L.-E. and Nilsson, C. 1988. Functional analysis of the suspension feeding system in mosquitoes (Diptera: Culicidae). *Ann. Entomol. Soc. Am.*, 81: 105-127.

Dajoz, R. 1976. Les Coléoptères Cerylonidae. Etude des espèces de la fauna Paléarctique. *Bull. Mus. Natl. Hist. Nat.*, (3), 360: 249-281.

Dampf, A. 1910. *Palaeopsylla klebsiana* n. sp., ein fossiler Floh aus dem baltischen Bernstein. *Schrift. Physik.-Okon. Ges. Koningsberg*, 51: 248-259.

Daniel, T.L. and Kingsolver, J.G. 1983. Feeding strategy and the mechanics of blood sucking in insects. *J. Theor. Biol.*, 105: 661-672.

Darlington, P.J. 1929. Notes on the structure and significance of *Palaeogyrinus*. *Psyche*, 36: 216-219.

Darwin, F. 1875. On the structure of the proboscis of *Ophideres fullonica*, an orange-sucking moth. *Quart. J. Micros. Sci.*, N.S., 15: 384-389.

Das, G.M. 1938. The musculature of the mouth-parts of insect larvae. *Quart. J. Micros. Sci.*, 80: 39-79.

Davies, A.L. and Tobin, P. 1984. The dragonflies of the world: a systematic list of the extant species of Odonata. Vol. 1. Zygoptera, Anisozygoptera. *Soc. Int. Odonatologica Rapid Comm., Suppl.*, 3: 1-127.

Davies, A.L. and Tobin, P. 1985. The dragonflies of the world: a systematic list of the extant species of Odonata. Vol. 2. Anisoptera. *Soc. Int. Odonatologica Rapid Comm., Suppl.*, 5: 1-151.

Davidson, J. 1914. On the mouth-parts and mechanism of suction in *Schizoneura lanigera*, Hausmann. *J. Linn. Soc.*, 32: 307-330.

Davidson, R.H. and Lyon, W.F. 1987. *Insect Pests of Farm, Garden, and Orchard*, 8th edn. New York: John Wiley & Sons. 640 p.

Davies, L. 1974. Evolution of larval head-fans in Simuliidae (Diptera) as inferred from the structure and biology of *Crozetia crozetensis* (Womersley) compared with other genera. *Zool. J. Linn. Soc.*, 55: 193-224.

Davies, R.G. 1958. Observations on the morphology of the head and mouthparts in the Thysanoptera. *Proc. Roy. Entomol. Soc. London*, (A), 33: 97-106.

Davis, C. 1936. Studies in Australian Embioptera. Part 1. Systematics. *Proc. Linn. Soc. New South Wales*, 61: 229-253.

Davis, D.R. 1967. A revision of the moths of the subfamily Prodoxinae. *U.S. Natl. Mus. Bull.*, 255: 1-170.

Davis, D.R. 1975. A review of Ochsenheimeriidae and the introduction of the cereal stem moth *Oschenheimeria vacculella* into the United States (Lepidoptera: Tineoidea). *Smithson. Contr. Zool.*, 192: 1-20.

Davis, D.R. 1978. A revision of the North American moths of the superfamily Eriocranioidea, with the proposal of a new family, Acanthopteroctetidae. *Smithson. Contr. Zool.*, 251: 1-131.

Davis, N.T. and Usinger, R.L. 1970. The biology and relationships of the Joppeicidae (Heteroptera). *Ann. Entomol. Soc. Am.*, 63: 577-587.

Day, R.W., Whittaker, W.G., Murray, C.G., Wilson, I.H. and Grimes, K.G. 1983. Queensland geology. A companion volume to the 1:2,500,000 scale geological map (1975). *Publs. Geol. Surv. Queensland*, 253: 1-194.

Day, W.C. 1956. Ephemeroptera. IN: Usinger, R.L., (Ed.), *Aquatic Insects of California, with Keys to North American Genera and California Species*, pp. 79-105. Berkeley: University of California Press.

DeGarcia, E.R. 1983. Insectos fosiles en la Formacion Ventana (Eoceno), Provincia de Neuquen. *Riv. Assn. Geol. Argentina*, **38**: 17-23.

DeGryse, J.J. 1915. Some modifications of the hypopharynx in lepidopterous larvae. *Proc. Entomol. Soc. Washington*, **17**: 173-179, pls. 17-19.

Deichmüller, L.V. 1886. Die Insekten aus dem lithographischen Schiefer im Dresdner Museum. *Mitt. Min. Geol. Prehist. Mus. Dresden*, **7**: 1-84.

Delachambre, J. 1965. Squelette et musculature cephaliques de la larve de *Limnius volkmari* Panz. (Col. Elminthidae). *Trav. Lab. Zool., Univ. Dijon*, **65**: 1-54, figs. 1-23.

Delamare-Deboutteville, C. and Massoud, Z. 1967. Un groupe panchronique: les collemboles. Essai critique sur *Rhyniella praecursor*. *Ann. Soc. Entomol. France*, 3: 625-629.

Delany, M.J. 1954. Studies on the life history and ecology of *Dilta littoralis* (Womersley, 1930) (Thysanura, Machilidae). *Trans. Roy. Entomol. Soc. London*, **105**: 31-63.

Delany, M.J. 1959. The life histories and ecology of two species of *Petrobius* Leach, *P. brevistylis* and *P. maritimus*. *Trans. Roy. Soc. Edinburgh*, **63**: 501-533.

Delany, M.J. 1960. A study on the post-embryonic development of *Machiloides delanyi* Wygodzinsky (Thysanura, Meinertellidae). *Proc. Roy. Entomol. Soc. London*, (A), **36**: 81-87.

Delanoue, P. and Arambourg, Y. 1967. Contribution a l'etude en laboratoire de *Pnigalio mediterraneus* (Hym. Chalcidoidea Eulophidae). *Ann. Soc. Entomol. France*, N.S., 3: 909-927.

Delevoryas, T. 1968. Investigations of North American cycadeoids: structure, ontogeny and phylogenetic considerations of cones of Cycadeoidea. *Palaeontographica*, (B). **121**: 122-133.

Deligne, J. 1965. Morphologie et fonctionnement des mandibules chez les soldats des termites. *Biol. Gabon.*, 1: 179-186.

Dell, J.A. 1905. The structure and life history of *Psychoda sexpunctata*, Curtis. *Trans. Entomol. Soc. London*, **1905**: 293-311.

De Lotto, G. 1974. On the status and identity of the cochineal insects (Homoptera: Coccoidea: Dacrylopiidae). *J. Entomol. Soc. So. Africa*, 37: 167-193.

De Marzo, L. 1976a. Studi sulle larve dei Coleotteri Ditiscidi. IV. Morfologia de tre stadi larvali di *Copelatus haemorrhoidalis* F. *Entomologica*, 12: 89-106.

De Marzo, L. 1976b. Studi sulle larve dei Coleotteri Ditiscidi. V. Note morfologiche sulle larve di tre specie del genere *Laccophilus* Leach. *Entomologica*, 12: 107-129.

De Marzo, L. 1976c. Studi sulle larve dei Coleotteri Ditiscidi. VI. Studio per fini sistematici del comportamento dei caratteri delle mandibole nelle larve di alcune specie della subf. Colymbetinae. *Entomologica*, 12: 179-198.

De Marzo, L. 1977a. Studi sulle larve dei Coleotteri Ditiscidi. VII. Considerazioni sul significato evolutivo del comportamento dei caratteri delle mandibole nelle larve di alcune specie della subf. Dytiscinae. *Entomologica*, 13: 71-84.

De Marzo, L. 1977b. Studi sulle larve dei Coleotteri Ditiscidi. VIII. Morfologia dei tre stadi larvali di *Oreotytes rivalis* Gyll. e *Hyphydrus aubei* Ganglb. e considerazioni sul comportamento di alcuni caratteri esoscheletrici nelle larve della subf. Hydroporinae. *Entomologica*, 13: 85-119.

De Marzo, L. 1978. Studi sulle larve dei Coleotteri Ditiscidi. IX. Morfologia delle mandibole delle larve in alcune specie delle subff. Laccophilinae e Hydroporinae. Ipotesi sulla derivazione morfogenetica dei relativi modelli di mandibola. *Entomologica*, 14: 137-157.

De Marzo, L. 1979. Studi sulle larve dei Coleotteri Ditiscidi. X. Anatomia e funzionamento dell'apparato succhiante cibario-faringeo in alcune forme larvale delle subff. Dytiscinae, Colymbetinae, Laccophilinae e Hydroporinae. *Entomologica*, 15: 5-72.

Demoll, R. 1908. Die Mundteile der solitaren Apiden. *Z. Wiss. Zool.*, 91: 1-51.

Demoulin, G. 1953. A propos d'*Hexagenites weyenberghi* Scudder, ephemeroptère du jurassique supérior de Solenhofen. *Bull. Inst. Roy. Sci. Nat. Belgique*, 25: 1-8.

Demoulin, G. 1954a. Les ephemeropteres jurassiques du Sinkiang. *Bull. Ann. Soc. Entomol. Belgique*, 90: 322-326.

Demoulin, G. 1954b. Essai sur quelques ephemeropteres fossiles adultes. *Vol. Jubil. Victor van Straelen*, 1: 547-574.

Demoulin, G. 1956a. *Electrogenia dewalschii* n.gen. n.sp. Ephémeroptère fossil de l'ambre. *Bull. Inst. Roy. Sci. Nat. Belg.*, 32: 95-100.

Demoulin, G. 1956b. Nouvelle recherches sur *Triplosoba pulchella* (Brongniart). *Bull. Inst. Rjoy. Sci. Nat. Belgique*, 32: 1-8.

Demoulin, G. 1965. Contribution à la conaissance des Ephéméroptères de l'ambre Oligocène de la Baltique. *Entomol. Meddel.*, 34: 143-153.

Demoulin, G. 1966. Remarques sur les Ephéméroptères Misthodotidae d'Europe et sur leurs rapports avec autres Ephéméroptères permiens. *Bull. Inst. Roy. Sci. Nat. Belgique*, 42: 1-5.

Demoulin, G. 1967. Contribution à la'étude morphologique, systématique et phylogénique des Ephéméroptères jurassiques d'Europe centrale. IV. Hexagenitidae et Paedephemeridae. *Bull. Inst. Roy. Sci. Nat. Belgique*, 43: 1-9.

Demoulin, G. 1968. Deuxième contribution à la conaissance des Ephémeroptères de l'ambre Oligocène de la Baltique. *Deut. Entomol. Z.*, N.F., 15: 233-276.

Demoulin, G. 1970. Quelques remarques sur certains Ephemeroptera triasiques et jurassiques. *Bull. Inst. Roy. Sci. Nat. Belgique*, 45: 1-10.

Denis, J.R. and Bitsch, J. 1973. Morphologie de tête des insectes. IN: Grasse, P.-P., (Ed.), *Traite de Zoologie; Anatomie, Systematique, Biologie*, 8(1): 1-593. Paris: Masson et Cie.

Dennell, R. 1942. The structure and function of the mouth-parts, rostrum and fore-gut of the weevil *Calandra granaria* L. *Phil. Trans. Roy. Soc. London*, (B), 231: 247-291.

Denning, D.G. 1956. Trichoptera. IN: Usinger, R.L., (Ed.), *Aquatic Insects of California, with Keys to North American Genera and Californian Species*, pp. 237-270. Berkeley: University of California Press.

Deoras, P.J. 1943. On the comparative morphology and evolution of adult Trichoptera. *Indian J. Entomol.*, 5: 177-188.

Deoras, P.J. 1944. On the comparative morphology and evolution of adult Trichoptera, part II. Internal morphology. *Indian J. Entomol.*, 6: 35-48.

Dethier, V.G. 1937. Gustation and olfaction in lepidopterous larvae. *Biol. Bull.*, 72: 7-23.

Dethier, V.G. 1942. The dioptric apparatus of lateral ocelli. I. *J. Cell. Comp. Physiol.*, 19: 301-303.

Dethier, V.G. 1943. The dioptric apparatus of lateral ocelli. II. *J. Cell. Comp. Physiol.*, 22: 115-126.

Dethier, V.G. 1954. Evolution of feeding preferences in phytophagous insects. *Evolution*, 8: 33-54.

Dethier, V.G. 1959. The nerves and muscles of the proboscis of the blow fly *Phormia regina* Meigen in relation to feeding responses. *Smithson. Misc. Collns.*, 137: 157-174.

Dettmann, M.E. 1986. Early Cretaceous palynoflora of subsurface strata correlative with the Koonwarra Fossil Bed, Victoria. *Mem. Assn. Australas. Palaeontol.*, 3: 79-110.

Devitt, B.D. and Smith, J.J.B. 1985. Action of mouthparts during feeding in the dark-sided cutworm, *Euxoa messoria* (Lepidoptera: Noctuidae). *Can. Entomol.*, 117: 343-349.

DeVries, P.J. 1983. *Papilio cresphontes* (lechera, papilio grande, giant swallowtail). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 751-752. Chicago: University of Chicago Press.

Dewitz, H. 1882. Ueber die Fürung an den Körperanhängen der Insecten. *Berl. Entomol. Z.*, 26: 51-66.

Dezaly, F. 1960. Etude sur le squelette cephalique et les genitalias de deux especes d'ascalaphes. *Trav. Lab. Zool., Univ. Dijon*, 36: 1-19, figs. 1-34.

Dickerson, G. and Lavoipierre, M.M.J. 1959. Studies on the methods of feeding of blood-sucking arthropods. II. The method of feeding adopted by the bedbug (*Cimex lectularis*) when obtaining a blood-meal from the mammalian host. *Ann. Trop. Med. Parasitol.*, 53: 347-357.

Dietrich, H.-G. 1976. Zur Entstehkung und Erhaltung von Bernstein-Lagerstätten--2. Bernstein-Lagerstätten im Libanon. *Neues Jb. Geol. Paläont. Abh.*, 151: 101-118.

Dimmock, G. 1881. Anatomy of the mouth-parts and of the suctorial apparatus of *Culex*. *Psyche*, 3: 231-242, pl. 1.

Dirsch, V.M. 1965. Revision of the family Pneumoridae (Orthoptera: Acridoidea). *Bull. Brit. Mus. Nat. Hist. (Entomol.)*, 15: 323-396.

Disney, R.H.L. 1987. Four species of scuttle fly (Diptera: Phoridae) from Dominican amber. *Pan-Pac. Entomol.*, **63**: 377-380.

Dixon, A.F.G. 1975. Aphids and translocation. IN: Zimmermann, M.H. and Milburn, J.A., (Eds.), *Transport in Plants. Phloem Transport.* 1: 154-170. Berlin: Springer-Verlag.

Djamin, A. and Pathak, M.D. 1967. Role of silica in resistance to Asiatic rice borer, *Chilo suppressalis* (Walker), in rice varieties. *J. Econ. Entomol.*, **60**: 347-351.

Dlussky, G.M. 1975. Family Formicidae. IN: Rasnitsyn, A.P., "Hymenoptera Apocrita of the Mesozoic." *Trans. Paleontol. Inst.*, **147**: 114-122.

Dlussky, G.M. 1983. A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between the ants and the scolioids. *Paleontol. J.*, **1983**(3): 65-78.

Dlussky, G.M. 1987. New Formicoidea (Hymenoptera) of the Upper Cretaceous. *Paleontol. J.*, **21**(1): 146-150.

Dlussky, G.M. 1988. Ants from (Paleocene?) Sakhalin amber. *Paleontol. J.*, **22**(1): 50-61.

Dmitriev, V.J. and Zherikin, V.V. 1988. Changes in the familial diversity of insects and a demonstration of the method of data analysis. IN: Ponomarenko, A.G., (Ed.), *The Mesozoic Biocoenotic Crisis in the Evolution of Insects*, pp. 208-215. Moscow: Academy of Sciences. [In Russian.]

Doeksen, J. 1941. Bijdrage tot de vergelijkende morphologie der Thysanoptera. *Meded. Landbouwhoog. Wagen.*, **45**: 1-114.

Dogra, G.S. 1967. Studies on the structure of the head, mouth-parts and their musculature in *Hippobosca maculata* Leach (Diptera: Pupipara). *Zool. Anz.*, **178**: 224-236.

Dohler, W. 1915. Die aussereuropaischen Trichopteren der Leipziger Universitats-Sammlung. *Deut. Entomol. Z.*, **1915**: 397-412.

Dohrn, A. 1867. Zur Kenntnis der Insekten in den Primärformationen. *Palaeontographica*, **16**: 129-135.

Dolin, V.G. 1973. Fossil forms of click-beetles (Elateridae, Coleoptera) from the Lower Jurassic of Soviet central Asia. IN: *The Insect Fauna of Moldavia and their Biology*, pp. 71-82. Kishniev, USSR: Shtiintsa Press. [In Russian.]

Donges, J. 1954. Der Kopf von *Cionus scrophulariae* L. Curculionidae). *Zool. Jb. (Anat.)*, 74: 1-76.

Dorf, E. 1967. Cretaceous insects from Labrador. 1. Geologic occurrence. *Psyche*, 74: 267-269.

Dorsey, C.K. 1943. The musculature of the labrum, labium, and pharyngeal region of adult and immature Coleoptera. *Smithson. Misc. Collns.*, 103: 1-42.

Doutt, R.L. 1973. The fossil Mymaridae (Hymenoptera: Chalcidoidea). *Pan-Pac. Entomol.*, 49: 221-228.

Doutt, R.L. and Viggiani, G. 1968. The classification of the Trichogrammatidae (Hymenoptera: Chalcidoidea). *Proc. California Acad. Sci.*, (4), 35: 477-586.

Downes, J.A. 1955. The food habits and description of *Atrichopogon pollinivorous* sp.n. (Diptera: Ceratopogonidae). *Trans. Roy. Entomol. Soc. London*, 106: 439-453.

Downes, J.A. 1958. The feeding habits of biting flies and their significance in classification. *Ann. Rev. Entomol.*, 3: 249-266.

Downes, J.A. 1971. The ecology of blood-sucking Diptera: an evolutionary perspective. IN: Fallis, A.M., (Ed.), *Ecology and Physiology of Parasites*, pp. 232-258. London: University of Toronto Press.

Downes, J.A. 1974. The feeding habits of adult Chironomidae. *Entomol. Tidskr.*, 95: 84-90.

Downes, J.A. 1977. Evolution of feeding habits in Ceratopogonidae. *Mosquito News*, 37: 279-280.

Downes, J.A. 1978. Feeding and mating in the insectivorous Ceratopogoninae (Diptera). *Mem. Entomol. Soc. Canada*, 104: 1-62.

Downes, J.A. and Smith, S.M. 1969. New or little-known feeding habits in Empididae (Diptera). *Can. Entomol.*, 101: 404-408.

Downes, J.A. and Wirth, W.W. 1981. Ceratopogonidae. IN: McAlpine, J.F., et al., "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 393-422.

Downes, W.L., Jr. 1963. A reinterpretation of certain head structures in calypterate Diptera. *Proc. Entomol. Soc. Washington*, 65: 293-298.

Downes, W.L., Jr. and Dahlem, G.A. 1987. Keys to the evolution of Diptera: role of Homoptera. *Environ. Entomol.*, 16: 847-854.

Doyle, J.A. and Donoghue, M.J. 1987. The origin of angiosperms: a cladistic approach. IN: Friis, E.M., Chaloner, W.G. and Crane, P.R., (Eds.), *The Origins of Angiosperms and their Biological Consequences*, pp. 17-49. New York: Cambridge University Press.

Doyle, J.A. and Hickey, L.J. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. IN: Beck, C.B., (Ed.), *Origin and Early Evolution of Angiosperms*, pp. 139-206. New York: Columbia University Press.

Doyen, J.T. 1966. The skeletal anatomy of *Tenebrio molitor* (Coleoptera: Teneobrionidae). *Misc. Publ. Entomol. Soc. Am.*, 5: 101-150.

Drake, C.J. and Davis, N.D. 1958. The morphology and systematics of the Piesmatidae (Hemiptera), with keys to world genera and American species. *Ann. Entomol. Soc. Am.*, **51**: 567-581.

Drake, C.J. and Davis, N.D. 1959. The morphology, phylogeny, and higher classification of the family Tingidae, including the description of a new genus and species of the subfamily Vianaidinae (Hemiptera: Heteroptera). *Entomol. Am.*, 39: 1-100.

Drinnan, A.N. and Chambers, T.C. 1986. Flora of the Lower Cretaceous Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Mem. Assn. Australas. Palaeontol.*, 3: 1-77.

Duckworth, W.D. 1973. The Old World Stenomidae: A preliminary survey of the fauna, notes on relationships, and revision of the genus *Eriogenes* (Lepidoptera: Gelechioidea). *Smithson. Contr. Zool.*, 147: 1-21.

Duda, O., 1934a. Periscelidae. IN: Lindner, E., (Ed.), *Die Fliegen der Palaearktischen Region*, **58a**: 1-13. Stuttgart: E. Schweizerbart's-che Verlagsbuchhandlung.

Duda, O., 1934b. Astiidae. IN: Lindner, E., (Ed.), *Die Fliegen der Palaearktischen Region*, **58b**: 1-15, pl. 1. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Duda, O., 1934c. Curtonotidae. IN: Lindner, E., (Ed.), *Die Fliegen der Palaearktischen Region*, **58d**: 1-5. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Duda, O., 1934d. Diastatidae. IN: Lindner, E., (Ed.), *Die Fliegen der Palaearktischen Region*, **58e**: 1-1-18, pls. 1-2. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Dukas, R. and Schmida, A. 1989. Correlation between color, size and shape of Israeli crucifer flowers and relationships to pollinators. *Oikos*, **54**: 281-286.

Dumbleton, L.J. 1952. A new genus of seed-infesting micropterygid moths. *Pac. Sci.*, 6: 17-29.

Dunbar, C.O. and Tillyard, R.J. 1924. Kansas Permian insects. Part 1. The geologic occurrence and the environment of the insects, with a description of a new palaeodictyopterid. *Am. J. Sci.*, (5), 39: 171-209, pls. 1-2.

Duncan, C.D. 1939. A contribution to the biology of North American vespine wasps. *Stanford Univ. Publ., Biol. Ser.*, 8: 1-272.

Duncan, C.O. 1922. The North American species of *Phylloxera* infesting oak and chestnut (Hemiptera, Phylloxeridae). *Can. Entomol.*, 54: 267-276.

Dunstan, B. 1924. Concluding note. *Publs. Queensland Geol. Surv.*, 273: 235-242.

DuPorte, E.M. 1946. Observations on the morphology of the face in insects. *J. Morphol.*, 79: 371-417.

DuPorte, E.M. 1956. The median facial sclerite in larval and adult Lepidoptera. *Proc. Roy. Entomol. Soc. London*, (A), 31: 109-116.

DuPorte, E.M. 1957. The comparative morphology of the insect head. *Ann. Rev. Entomol.*, 2: 55-70.

DuPorte, E.M. 1958. Are there preoral structures in insects? *Proc. 10th Int. Congr. Entomol.*, 1: 479-485.

DuPorte, E.M. 1962a. The morphology of the insect mandible. *Can. J. Zool.*, 40: 1229-1231.

DuPorte, E.M. 1962b. Origin of the gula in insects. *Can. J. Zool.*, 40: 381-384.

DuPorte, E.M. 1962c. The anterior tentorial arms in insects and their significance in interpreting the morphology of the cranium of the cicadas. *Can. J. Zool.*, 40: 137-143.

DuPorte, E.M. 1977. *Manual of Insect Morphology*. Huntington, New York: Robert E. Krieger Publ. Co. 224 p.

DuPorte, E.M. and Bigelow, R.S. 1953. The clypeus and epistomal suture in Hymenoptera. *Can. J. Zool.*, 31: 20-29.

Durand, J.-B. 1955. Contribution a l'etude des Trichoptérès. *Trav. Lab. Zool. Univ. Dijon*, 9: 1-45, figs. 1-42.

Durden, C.J. 1966. Oligocene lake deposits in central Colorado and a new fossil insect locality. *J. Paleontol.*, 40: 216-219.

Durden, C.J. 1978. A dasyleptid from the Permian of Kansas, *Lepidodasypus sharovi* n. gen., n. sp. (Insecta: Thysanura: Monura). *Pearce-Sellards Ser., Texas Mem. Mus.*, 30: 1-9.

Durden, C.J. 1984. North American provincial insect ages for the continental last half of the Carboniferous and first half of the Permian. *C.R. Neuv. Congr. Int. Strat. Geol. Carbonifère*, 2: 606-612.

Durden, C.J. and Rose, H. 1978. Butterflies from the Middle Eocene: the earliest occurrence of fossil Papilionoidea (Lepidoptera). *Pearce-Sellards Set., Texas Mem. Mus.*, 29: 1-25.

Dussourd, D.E. and Eisner, T. 1987. Vein-cutting behavior: insect counterploy to the latex defense of plants. *Science*, 237: 898-901.

Dyar, H.G. 1896. Note on the head setae of lepidopterous larvae, with special reference to the appendages of *Pterophora melsheimerii*. *J. New York Entomol. Soc.*, 4: 92-93.

Dybas, H.S. and Lloyd, M. 1974. The habitats of 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). *Ecol. Mon.*, 44: 279-324.

Eassa, Y.E.E. 1963a. The musculature of the head appendages and the cephalic stomodaeum of *Pieris brassicae* (Lepidoptera: Pieridae). *Ann. Entomol. Soc. Am.*, 56: 500-510.

Eassa, Y.E.E. 1963b. Metamorphosis of the cranial capsule and its appendages in the cabbage butterfly, *Pieris brassicae*. *Ann. Entomol. Soc. Am.*, 56: 510-521.

Eastham, L.E.S. 1929. The post-embryonic development of *Phaenoserphus viator* Hal. (Proctotrypoidea), a parasite of the larva of *Pterostichus niger* (Carabidae), with notes on the anatomy of the larva. *Parasitology*, 21: 1-21, pls. 1-3.

Eastham, L.E.S. and Eassa, Y.E.E. 1955. The feeding mechanism of the butterfly *Pieris brassicae* L. *Phil. Trans. Roy. Soc. London*, (B), 239: 1-43.

Eastop, V.F. 1966. The mouthparts of some common genera of Aphidiinae (Hymenoptera: Braconidae). *Proc. Roy. Entomol.Soc. London*, (A), 41: 42-44.

Eastop, V.F. 1973. Deductions from the present day host plants of aphids and related insects. IN: Van Emden, H.F., (Ed.), *Insect/ Plant Relationships*, pp. 157-178. London: Blackwell Scientific Publications.

Edmunds, F.H. and Gallois, R.W. 1965. *The Wealden District*, 4th edn. Brit. Reg. Geol. London: Geological Survey and Museum. 101 pp.

Edmunds, G.F., Jr. 1972. Biogeography and evolution in the Ephemeroptera. *Ann. Rev. Entomol.*, 17: 21-42.

Edmunds, G.F., Jr. 1982. Ephemeroptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 330-338. New York: McGraw-Hill Book Co.

Edmunds, G.F., Jr. 1984. Ephemeroptera. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 94-125. Dubuque: Kendall/Hunt Publ. Co.

Edmunds, J.S. 1961. The action and composition of the saliva of an assassin bug, *Platymeris rhadamanthus* Gaerst. (Hemiptera, Reduviidae). *J. Exp. Biol.*, 38: 61-77.

Edwards, J.S. 1960. Insect assassins. *Sci. Am.*, 202: 72-78.

Edwards, P.J. and Wratten, S.D. 1980. Ecology of insect-plant interactions. *Inst. Biol., Stud. Biol.*, 121: 1-60.

Ehrlich, P.R. 1958a. The integumental anatomy of the monarch butterfly *Danaus plexippus* L. (Lepidoptera: Danaiidae). *Univ. Kansas Sci. Bull.*, 38: 1315-1349.

Ehrlich, P.R. 1958b. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). *Univ. Kansas Sci. Bull.*, 39: 305-370.

Ehrlich, P.R. and Davidson, S.E. 1961. The internal anatomy of the monarch butterfly, *Danaus plexippus* L. (Lepidoptera: Nymphalidae). *Microentomology*, 24: 85-133.

Ehrlich, P.R. and Ehrlich, A.H. 1962. The head musculature of the butterflies (Lepidoptera: Papilioinoidea). *Microentomology*, 25: 1-85.

Ehrlich, P.R. and Raven, P.H. 1964. Butterflies and plants: a study in coevolution. *Evolution*, 18: 586-608.

Ehrlich, P.R. and Raven, P.H. 1967. Butterflies and plants. *Sci. Am.*, 216: 104-113.

Eichwald, E. 1864. *"Lethaea Rossica" ou Palaeontologie de la Russie.* 11: 1192-1195. Stuttgart.

Eidmann, H. 1925. Vergleichend-anatomische Studien über die Pharynxmuskulatur der Insekten. *Zool. Anz.*, 62: 49-64.

Eisenbeis, G. and Wichard, W. 1988. *Atlas on the Biology of Soil Arthropods.* Berlin: Springer-Verlag. 437 pp.

Eisenberg, J.F. 1981. *The Mammalian Radiations.* Chicago: University of Chicago Press. 610 pp.

Ekblom, T. 1926. Morphological and biological studies of the Swedish families of Hemiptera-Heteroptera. Part 1. The families Saldidae, Nabidae, Lygaeidae, Hydrometridae, Veliidae and Gerridae. *Zool. Bier.*, 10: 29-179.

Elbel, R.E. 1951. Comparative studies on the larvae of certain species of fleas (Siphonaptera). *J. Parasitol.*, 37: 119-128.

Elliott, E.A. 1922. Monograph of the hymenopterous family, Stephanidae. *Proc. Zool. Soc. London*, 1922: 705-831.

Elliott, J.M. and Elliott, J.I. 1967. The structure and possible function of the buccopharyngeal teeth of *Sigara dorsalis* (Leach) (Hemiptera: Corixidae). *Proc. Roy. Entomol. Soc. London*, (A), 42: 83-86.

Elsey, K.D. and Stinner, R.E. 1971. Biology of *Jalysus spinosus*, an insect predator found on tobacco. *Ann. Entomol. Soc. Am.*, 64: 779-783.

Eltringham, H. 1923. On the larva of *Pterocroce storeyi*, With. (Nemopteridae). *Trans. Entomol. Soc. London*, 1923: 263-268.

Elzinga, R.J. and Broce, A.B. 1986. Labellar modifications of Muscomorpha flies (Diptera). *Ann. Entomol. Soc. Am.*, 79: 150-209.

Emden, F. van 1932. Die Larven von *Discoloma cassideum* Reitt. (Col. Colyd.) und *Skwarraia paradoxa* Lac. (Col. Chrysom.). *Zool. Anz.*, 101: 1-17.

Emden, F. van 1950. *Mormotomyia hirsuta* Austen (Diptera) and its systematic position. *Proc. Roy. Entomol. Soc. London*, (B), 19: 121-128.

Emerson, A.E. 1965. A review of the Mastotermitidae (Isoptera), including a new fossil species from Brazil. *Am. Mus. Novit.*, 2236: 1-46.

Emerson, A.E. 1967. Cretaceous insects from Labrador. 3. A new genus and species of termite (Isoptera: Hodotermitidae). *Psyche*, 74: 276-289.

Emerson, A.E. 1969. A revision of the Tertiary fossil species of Kalotermitidae (Isoptera). *Am. Mus. Novit.*, 2359: 1-57.

Emerson, A.E. and Krishna, K. 1975. The termite family Serritermititidae (Isoptera). *Am. Mus. Novit.*, 25: 1-31.

Emerson, K.C. 1982. Mallophaga. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 409-415. New York: McGraw-Hill Book Co.

Emery, W.T. 1913. Morphology and biology of *Simulium vittatum* and its distrubution in Kansas. *Kansas Univ. Sci. Bull.*, 8: 323-362, pls. 38-42.

Emmel, T.C. 1971. Symbiotic relationship of an Ecuadorian skipper (Hesperiidae) and *Maxillaria ontoglossum*. *J. Lepid. Soc.*, 25: 20-22.

Enderlein, G. 1911. Die fossilen Copeognathen und ihre Phylogenie. *Palaeontographica*, 11: 279-365, pls. 21-27.

English, K.M.I. 1947. Notes on the morphology and biology of *Apiocera maritima* Hardy (Diptera, Apioceridae). *Proc. Linn. Soc. New South Wales*, 71: 296-302.

Enslin, X. 1917. Die Tenthredinoidea Mitteleuropas. *Deut. Entomol. Z.*, 1917: 537-759.

Erlanson, C.D. 1930. The attraction of carrion flies tc *Tetraplodon* by an odoriferous secretion of the hypophysis. *Bryologist*, 33: 13-14.

Erwin, T.L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.*, 36: 74-75.

Essig, E.O. 1937. Order Homoptera. IN: Carpenter, F.M., et al., Insects and arachnids from Canadian amber. *Univ. Toronto Stud. Geol. Ser.*, 40: 56-62.

Etheridge, R.J. and Olliff, A.S. 1890. The Mesozoic and Tertiary insects of New South Wales. *Mem. Geol. Surv. New South Wales Paleontol.*, 7: 1-13, pls. 1-2.

Evans, A.W. 1921. On the structure and occurrence of maxillulae in the orders of insects. *J. Linn. Soc. London*, 34: 429-456.

Evans, H.E. 1959. The larvae of Pompilidae (Hymenoptera). *Ann. Entomol. Soc. Am.*, 52: 430-444.

Evans, H.E. 1963. A new family of wasps. *Psyche*, 70: 7-16.

Evans, H.E. 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bull. Mus. Comp. Zool.*, 132: 1-222.

Evans, H.E. 1966. Discovery of the female *Plumarius* (Hymenoptera: Plumariidae). *Psyche*, 73: 229-237.

Evans, H.E. 1969. Three new Cretaceous aculeate wasps (Hymenoptera). *Psyche*, 76: 251-261.

Evans, H.E. 1973. Cretaceous aculeate wasps from Taimyr, Siberia (Hymenoptera). *Psyche*, 80: 166-178.

Evans, H.E. 1984. *Insect Biology: A Textbook of Entomology*. Reading, MA: Addison-Wesley Publishing Co. 436 pp.

Evans, J.W. 1928. Notes on *Nesomachilis maoricus* Tillyard, with particulars of a new sense-organ. *Trans. Proc. New Zealand Inst.*, 58: 375-378.

Evans, J.W. 1937. Morphology of the head of Homoptera. *Pap. Proc. Roy. Soc. Tasmania*, 1938: 1-20.

Evans, J.W. 1942. Further notes on the morphology of the insect head. *Trans. Roy. Soc. So. Aust.*, 66: 180-184.

Evans, J.W. 1956. Palaeozoic and Mesozoic Hemiptera. *Aust. J. Zool.*, 4: 165-258.

Evans, J.W. 1964. The periods of origin and diversification of the superfamilies of the Homoptera-Auchenorrhyncha as determined by a study of the wings of Palaeozoic and Mesozoic fossils. *Proc. Linn. Soc. London*, 175: 171-181.

Evans, J.W. 1973. The maxillary plate of Homoptera-Auchenorrhyncha. *J. Entomol.*, 48: 43-47.

Evans, J.W. 1975. The external features of the heads of leafhoppers (Homoptera, Cicadelloidea). *Rec. Aust. Mus.*, 29: 407-439.

Evans, M.E.G. 1961. The fronto-clypeal region and the stomodeum in Coleoptera. *Proc. Roy. Soc. London*, (A), 36: 159-162.

Evans, M.E.G. 1965a. The feeding method of *Cicindela hybrida* L. (Coleoptera: Cicindelidae). *Proc. Roy. Entomol. Soc. London*, (A), 40: 61-66.

Evans, M.E.G. 1965b. A comparative account of the feeding methods of the beetles *Nebria brevicollis* (F.) (Carabidae) and *Philonthus decorus* (Grav.) (Staphylinidae). *Trans. Roy. Soc. Edinburgh*, 66: 91-109.

Evans, M.E.G. 1965c. An interpretation of gular size in some adult Coleoptera. *Proc. Zool. Soc. London*, 144: 403-413.

Evans, M.E.G. and Forsythe, T.G. 1985. Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Caraboidea). *J. Zool., London*, (A), 206: 113-143.

Evenhuis, N.L. 1984. A reassessment of the taxonomic position of the fossil species *Protophthiria palpalis* and *P. atra* (Diptera: Bombyliidae). *Int. J. Entomol.*, 26: 157-161.

Evert, R.F., Eschrich, W., Medler, J.T. and Alfieri, F.J. 1968. Observations on penetration of linden branches by stylets of the aphid *Longistigma caryae*. *Am. J. Bot.*, 55: 860-874.

Fabricius, J.C. 1775. *Systema Entomologicae*. Flensburg and Lipsia. 832 pp.

Fabricius, J.C. 1790. Nova insectorum genera. *Skrift. Naturhis.*, 1: 213-228.

Fabricius, J.C. 1799. *Entomologia Systematica Emendata Aucta. Supplementum*. Hafnia. 52 pp.

Faegri, K. and van der Pijl, L. 1980. *The Principles of Pollination Ecology*, 3rd revised edn. Oxford: Pergamon Press. 244 pp.

Farenholz, H. 1936. Zur systematik der Anopluren. *Z. Parasitol.*, 9: 50-56.

Farnsworth, M.W. 1947. The morphology and musculature of the larval head of *Anopheles quadrimaculatus* Say. *Ann. Entomol. Soc. Am.*, 40: 137-151.

Felix, M. 1962. Recherches sur l'anatomie cephalique d'une larve de *Dixa* (*Paradixa*) (Diptere Nematocère). *Trav. Lab. Zool., Univ. Dijon*, 43: 1-43.

Fennah, R.G. 1952. On the classification of the Tettigometridae (Homoptera: Fulgoroidea). *Trans. Roy. Entomol. Soc. London*, 103: 239-255.

Fennah, R.G. 1952. A revision of *Bladina* Stal (Nogodinidae: Fulgoroidea). *Ann. Mag. Nat. Hist.*, (12), 5: 910-928.

Fennah, R.G. 1963. New fossil fulgorid Homoptera from the amber of Chiapas, Mexico. *Univ. California Publ. Entomol.*, 31: 43-48.

Fennah, R.G. 1987. A new genus and species of Cixiidae (Homoptera: Fulgoroidea) from Lower Cretaceous amber. *J. Nat. Hist.*, 21: 1237-1240.

Fernald, H.T. 1935. *Applied Entomology: An Introductory Textbook of Insects and Their Relation to Man.* New York: McGraw-Hill Book Company. 405 p.

Fernando, W. 1934. The development and homologies of the mouth-parts of the head-louse. *Quart. J. Micros. Sci.*, N.S., 76: 231-241.

Feroz, M. and Chaudhry, A. 1975. Studies on mandibles of some grasshoppers of Lahore. *Biologia*, 21: 211-225.

Ferrière, C. 1929. Chalcidens gallicoles de Java. *Ann. Soc. Entomol. France*, 98: 143-161.

Ferris, G.F. 1940. The morphology of *Plega signata* (Hagen) (Neuroptera: Mantispidae). *Microentomology*, 5: 33-56.

Ferris, G.F. 1941. Contributions to the knowledge of the Coccoidea (Homoptera). IX. A forgotten genus of the family Margarodidae from Baltic amber. *Microentomology*, 6: 6-10.

Ferris, G.F. 1942. Some observations on the head of insects. *Microentomology*, 7: 25-62.

Ferris, G.F. 1943a. The basic materials of the insect cranium. *Microentomology*, 8: 8-24.

Ferris, G.F. 1943b. Some fundamental concepts in insect morphology. *Microentomology*, 8: 2-7.

Ferris, G.F. 1944. On certain evolutionary tendencies in the heads of insects. *Microentomology*, 9: 78-84.

Ferris, G.F. 1947. The contradictions of the insect head. *Microentomology*, 12: 60-64.

Ferris, G.F. 1955. *Atlas of the Scale Insects of North America. Volume VII. The Families Aclerdidae, Asterolecaniidae, Conchaspididae, Dactylopiidae, and Lacciferidae.* Stanford, CA.: Stanford University Press. 233 p.

Ferris, G.F. and Pennebaker, P. 1939. The morphology of *Agulla adnixa* (Hagen) (Neuroptera: Raphidiidae). *Microentomology*, 4: 121-142.

Ferris, G.F. and Rees, B.E. 1939. The morphology of *Panorpa nuptialis* Gerstaecker (Mecoptera: Panorpidae). *Microentomology*, 4: 79-108.

Ferris, G.F. and Usinger, R.L. 1939. The family Polyctenidae (Hemiptera, Heteroptera). *Microentomology*, 4: 1-50.

Fieffé, C. 1965. Morphologie de la larve de *Speophyes lucidulus* Delarouzée. *Ann. Spéléol.*, 20: 401-407.

Fiori, G. 1949. Contributi alla conoscenza morfologica ed etologica dei Coleotteri. *Boll. Ist. Entomol., Univ. Bologna*, 17: 188-195.

Fitch, A. 1863. *Eighth report on the noxious and other insects of New York*. Albany.

Flamm, R.O., Coulson, R.N., Beckley, P., Pulley, P.E. and Wagner, T.L. 1989. Maintenance of a phloem-inhabiting guild. *Environ. Entomol.*, 18: 381-387.

Fleming, R.C. 1968. Head musculature of sphinx moths (Lepidoptera: Sphingidae). *Contrib. Am. Entomol. Inst.*, 3: 1-32.

Folsom, J.W. 1899. The anatomy and physiology of the mouth-parts of the collembolan, *Orchesella cincta* L. *Bull. Mus. Comp. Zool.*, 35: 1-39.

Folsom, J.W. 1900. The development of the mouth-parts of *Anurida maritima* Guer. *Bull. Mus. Comp. Zool.*, 36: 87-157.

Folsom, J.W. 1937. Order Collembola IN: Carpenter, F.M., et al., Insects and arachnids from Canadian amber. *Univ. Toronto Stud. Geol. Ser.*, 40: 14-17.

Foote, B.A. 1970. The larvae of *Tanypeza longimana* (Diptera: Tanypezidae). *Ann. Entomol. Soc. Am.*, 63: 235-238.

Forbes, A.R. 1969. The stylets of the green peach aphid, *Myzus persicae* (Homoptera: Aphididae). *Can. Entomol.*, 101: 31-41.

Forbes, A.R. 1972. Innervation of the stylets of the pear psylla, *Psylla pyricola* (Homoptera: Psyllidae), and the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). *J. Entomol. Soc. Brit. Columbia*, 69: 27-30.

Forbes, A.R. 1976. The stylets of the large milkweed bug, *Oncopeltus fasciatus* (Hemiptera: Lygaeidae), and their innervation. *J. Entomol. Soc. Brit. Columbia*, 73: 29-32.

Forbes, A.R. 1977. The mouthparts and feeding mechanisms of aphids. IN: Harris, K.F. and Maramorosch, K., (Eds.), *Aphids as Virus Vectors*, pp. 83-103. New York: Academic Press.

Forbes, A.R. and Mullick, D.B. 1970. The stylets of the balsam wooly aphid, *Adelges piceae* (Homoptera: Adelgidae). *Can. Entomol.*, **102**: 1074-1082.

Forbes, A.R. and Raine, J. 1973. The stylets of the six-spotted leafhopper, *Macrosteles fascifrons* (Homoptera: Cicadellidae). *Can. Entomol.*, **105**: 559-567.

Forbes, S.A. 1883. The food relations of the Carabidae and Cocinellidae. *Bull. Illinois St. Lab. Nat. Hist.*, 3: 153-160.

Forbes, W.T.M. 1910. A structural study of some caterpillars. *Ann. Entomol. Soc. Am.*, 3: 94-132.

Forbes, W.T.M. 1911. A structural study of the caterpillars. II. The Sphingidae. *Ann. Entomol. Soc. Am.*, 4: 261-279.

Forbes, W.T.M. 1923. The Lepidoptera of New York and neighboring states. Primitive forms, Microlepidoptera, pyraloids, *Bombyces*. *Cornell Univ. Agr. Exp. Stn. Mem.*, **68**: 1-729.

Ford, L.T. 1949. *A Guide to the Smaller British Lepidoptera*. London: South London Entomological and Natural History Society. 230 p.

Forrest, J.M.S. 1987. Galling aphids. IN: Minks, A.K. and Harrewijn, P., (Eds.), *Aphids: Their Biology, Natural Enemies and Control*, A: 341-353. Amsterdam: Elsevier.

Forsythe, T.G. 1982. Feeding mechanisms of certain ground beetles. *Coleopt. Bull.*, 36: 26-73.

Forsythe, T.G. 1983. Mouthparts and feeding of certain ground beetles (Coleoptera: Carabidae). *Zool. J. Linn. Soc.*, **79**: 319-376.

Fortner, G. 1937. Zur Ernährungsfrage der Simulium-Larve. *Z. Morphol. Okol. Tiere*, 32: 360-383.

Fotius-Jaboulet, M.C. 1961. Squlette et musculature cephaliques de la larve *Drusus trifidus* MacLachlan (Trichoptera Limnophilidae). *Trav. Lab. Zool., Univ. Dijon*, **40**: 1-54.

Fotius-Jaboulet, M.C. 1964. Description de la larve de *Rhyacophila praemorsa* McL. et comparison de cette larve a *Rhyacophila septentrionis* McL. *Trav. Lab. Zool., Univ. Dijon*, **62**: 1-13, figs.1-33.

Francois, J. 1959. Squelette et musculature cephaliques d'*Acerentomon propinquem* (Condé) (Ins. Protoures). *Trav. Lab. Zool., Univ. Dijon*, 29: 1-57, figs. 1-33.

Francois, J. 1969. Anatomie et morphologie cephalique des protoures (Insecta Apterygota). *Mem. Mus. Natl. Hist. Nat.*, 59: 1-144.

Francois, J. 1970. Squelette et musculature cephalique de *Campodea chardardi* Condé (Diplura: Campodeidae). *Zool. Jb. (Anat.)*, 87: 331-376.

Frankel, G. 1959. The raison d'etre of secondary substances. *Science*, 129: 1466-1470.

Frankie, G.W. and Daly, H.V. 1983. *Xylocopa gualanensis* (xicote, avispa carpintera, carpenter bee). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 777-779. Chicago: University of Chicago Press.

Franzen, J.L. 1985. Exceptional preservation of Eocene vertebrates in the lake deposit of Grube Messel (West Germany). IN: Whittington, H.B. and Conway Morris, S., (Eds.), *Extraordinary Fossil Biotas: Their Ecological and Evolutionary Significance*, pp. 181-186. London: The Royal Society.

Freeman, T.N. 1947. A new generic assignment for *Archips fumiferana* (Clemens, the spruce budworm (Lepidoptera, Tortricidae). *Can. Entomol.*, 79: 21-31.

Freeman, T.N. 1965. A lepidopterous leaf-mine from the Tertiary Period. *Can. Entomol.*, 97: 1069-1070.

Frew, J.G.H. 1923. On the morphology of the head capsule and mouthparts of *Chlorops taeniopus* Meig. (Diptera). *J. Linn. Soc.*, 35: 399-410.

Frey, R. 1913. Uber die munteile der Mycetophiliden, Sciariden, und Cecidomyiiden. *Acta Soc. Fauna Flora Fenn.*, 37: 1-54, pls. 1-3.

Frey, R. 1921. Studien uber den Bau des Mundes der niederen Diptera Schizophora nebst Bemerkungen uber die Systematik dieser Dipterengruppe. *Acta Soc. Fauna Flora Fenn.*, 48: 1-245, pls. 1-10.

Fric, A. 1901. Die thierischen Reste der Perucher Schichten. *Archiv. Naturwiss. Landesdurch. Böhm.*, 11: 163-180.

Friis, E.M. 1985. Structure and function in Late Cretaceous angiosperm flowers. *Biol. Skif. Danske Videns. Selsk.*, 25: 1-37.

Friis, E.M. 1989. VI. Palaeobotany. *Prog. Bot.*, **50**: 312-326.

Fritsch, A. 1882. Fossile Arthropoden aus der Steinkohlen- und kreideformation Böhmens. *Beitr. Palaönt. Oster.-Ung.*, **2**: 1-7, pls. 1-2.

Frochot, B. 1962. La larve de *Stenophylax permistus* McL. Trichoptera, Limnophilidae). *Trav. Lab. Zool., Univ. Dijon*, **42**: 1-16.

Froehlich, C.G. 1964. The feeding apparatus of the nymph of *Arthoplea congener* Bengtsson (Ephemeroptera). *Opusc. Entomol.*, **29**: 188-208.

Frost, S.W. 1925. The leaf-mining habit in the Hymenoptera. *Ann. Entomol. Soc. Am.*, **18**: 399-414, pls. 29-30.

Frost, S.W. 1959. *Insect Life and Insect Natural History*, 2nd edn. New York: Dover Publications. 526 p.

Fuchs, G.V. 1974. Die Gewinnung von Pollen und Nektar bei Kafern. *Natur. Mus.*, **104**: 45-54.

Fukuda, A. 1943. Larva of *Helota gemmata* Gorham. *Trans. Nat. Hist. Soc. Taiwan*, **33**: 15-18.

Fuller, M.E. 1934. The early stages of *Sciadocera rufomaculata* White (Dipt. Phoridae). *Proc. Linn. Soc. New South Wales*, **41**: 9-15.

Fuller, M.E. 1938. Notes on *Trichopsidea oestracea* (Nemestrinidae) and *Cyrtomorpha flaviscutellaris* (Bombyliidae)--two dipterous enemies of grasshoppers. *Proc. Linn. Soc. New South Wales*, **63**: 95-104.

Futuyma, D.J. and Gould, F. 1979. Associations of plants and insects in a deciduous forest. *Ecol. Mon.*, **49**: 33-50.

Gad, A.M. 1951. The head-capsule and mouth-parts in the Ceratopogonidae. *Bull. Soc. Fouad I Inst. Entomol.*, **35**: 17-75.

Gage, J.H. 1970. The larvae of the Coccinellidae. *Illinois Biol. Mon.*, **6(4)**: 1-62, pls. 1-6.

Gagné, R.J. 1973. Cecidomyiidae from Mexican amber (Diptera). *Proc. Entomol. Soc. Washington*, **75**: 169-171.

Gagné, R.J. 1977. Cecidomyiidae (Diptera) from Canadian amber. *Proc. Entomol. Soc. Washington*, **79**: 57-62.

Gagné, R.J. 1981. Cecidomyiidae. IN: McAlpine, J.F., et al., "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 257-292.

Gahan, C.J. 1908. On the larvae of *Trichentoma childreni*, Gray, *Melittotomma insulare*, Fairmaire, and *Dascillus cervinus*, Linn. *Trans. Roy. Entomol. Soc. London*, **1908**: 275-282.

Galil, J. 1978. Fig biology. *Endeavour*, N.S., **1**: 52-56.

Gall, J.-C. 1983. *Ancient Sedimentary Environments and the Habitats of Living Organisms: Introduction to Palaeoecology*. Berlin: Springer-Verlag. 219 pp.

Gall, L.F. and Tiffney, B.H. 1983. A fossil noctuid moth egg from the Late Cretaceous of eastern North America. *Science*, **219**: 507-509.

Gangrade, G.A. 1965. Studies on the head of *Necrosia sparaxes* Westwood (Phasmida: Phasmidae). *Indian J. Entomol.*, **27**: 77-84.

Gangwere, S.K. 1960. The use of the mouthparts of Orthoptera during feeding. *Entomol. News*, **71**: 193-206.

Gangwere, S.K. 1965. The structural adaptations of mouthparts in Orthoptera and allies. *Eos*, **41**: 67-85.

Gangwere, S.K. 1966. Relationships between the mandibles, feeding behavior and damage inflicted on plants by the feeding of certain acridids (Orthoptera). *Mich. Entomol.*, **1**: 13-16.

Gangwere, S.K. 1972. Host finding and feeding behavior in the Orthopteroidea, especially as modified by food availability: a review. *Rev. Univ. Madrid*, **21**: 107-158.

Gardiner, B.G. 1961. New Rhaetic and Liassic beetles. *Palaeontology*, **4**: 87-88

Gardner, C.F. and Nielsen, L.T. 1973. Functional interrelationships of the substructures of the mouthparts of larval mosquitoes. *Mosq. Syst.*, **5**: 183-193.

Gardner, C.F., Nielsen, L.T. and Knight, K.L. 1973. Morphology of the mouthparts of larval *Aedes communis* (DeGeer) (Diptera: Culicidae). *Mosq. Syst.*, **5**: 163-182.

Gardner, J.C.M. 1946. Larvae of Cantharoidea (Coleoptera). *Indian J. Entomol.*, **8**: 121-129.

Garman, H. 1896. The asymmetry of the mouth-parts of Thysanoptera. *Am. Nat.*, **30**: 591-593.

Garrido-Megias, A. and Rios Aragües, L.M. 1972. Síntesis geológica del Secundario y Terciario entre los rios Cinca y Segre. *Boln. Geol. Min. Inst. Geol. Min. España*, **83**: 1-47.

Gauld, I. and Bolton, B., (Eds.). 1988. *The Hymenoptera*. Oxford: Oxford University Press. 332 pp.

Geinitz, F.E. 1880. Der Jura von Dobbertin im Mecklenburg und seine Verstein erungen. *Z. Deut. Geol. Ges. Berlin*, 32: 510-535.

Geinitz, F.E. 1884. 5. Ueber die Fauna des Dobbertiner Lias. *Z. Deut. Geol. Ges. Berlin*, 36: 566-583, pl. 13.

Geise, O. 1883. Die Mundtheile der Rhychoten. *Arch. Naturges.*, 49: 315-373.

Genay, A. 1953. Contribution a l'etude des Nevropteres. *Trav. Lab. Zool., Univ. Dijon*, 3: 1-29.

Genthe, K.W. 1898. Die Mundwerkzeuge der Mikrolepidopteren. *Zool. Jb. (Syst., Geog., Biol.)*, 10: 373-471.

George, V.P. 1952. On some arthropod microfossils from India. *Agra Univ. J. Res.*, 1: 83-108.

George, V.P. 1969. Record of an apparently new microfossil species (Insecta: Corrodentia) from the Cretaceous Limestone Clay, Seminar Hills, Nagpur (India). *Bull. Entomol.*, 10: 1-3.

Gerig, L. 1960. Zur Morphologie der Larvenstadien einiger parasitischer Hymenopteren des Grauen Larchwicklers (*Zeiraphera griseana* Hubner). *Z. Angew. Entomol.*, 46: 121-177.

Germar, E.F. 1813. Insekten in Bernstein einge schlossen, beschrieven aus dem academischen Mineralien-Cabinet zu Halle. *Mag. Entomol. Germar*, 1: 11-18.

Germar, E.F. 1839. Die viesteinerten Insecten Solenhofens. *Nova Acta Acad. Leop. Carol.*, 19: 187-222, pls. 21-23.

Germar, E.G. and Berendt, G.C. 1856. *Zusätzen von A. Menge. Die im Bernstein befindlichen Hemipteren und Orthopteren der Vorwelt*, pp. 1-40. Königsberg.

Geyer, O.F. and Gwinner, M.P. 1979. Die Schwäbische Alb und ihr Vorland. *Sammlung Geol. Führer*, 67: 1-271, pls. 1-14.

Ghilarov, M.S. 1956. Soil as the environment of the invertebrate transition from the aquatic to the terrestrial life. *Proc. Sixth Int. Congr. Sci. Sol.*, 3: 307-313.

Ghilarov, M.S., (Ed.) 1964. *Determination of Soil Habitats for Larval Insects*. Moscow: Academy of Sciences. 919 pp. [In Russian.]

Gibbins, E.G. 1938. The mouth-parts of the female in *Simulium damnosum* Théobald, with special reference to the transmission of *Onchocerca volvulus* Leuckart. *Ann. Trop. Med. Parasitol.*, 32: 9-20.

Giebel, C.G. 1856. *Fauna der Vorwelt mit seter Berücksichtigung der lebenden Thiere monographisch dargestellt. 2. Gliederthiere. 1. Abt. Insekten und Spinnen.* Leipzig. 411 pp.

Giebel, C.G. 1862. Wirbeltier- und Insektenreste im Bernstein. *Z. Ges. Naturwiss.*, 20: 311-321.

Giguère, L.A. and Dill, L.M. 1983. Kinematic analysis of the trophic apparatus of larval *Chaoborus trivittatus* (Diptera: Chaoboridae). *Ann. Entomol. Soc. Am.*, 76: 981-984.

Gilbert, F.S. 1981. Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecol. Entomol.*, 6: 245-262.

Gilbert, F.S. 1988. Ecomorphology of hoverflies (Diptera: Syrphidae). *Proc. 18th Int. Congr. Entomol.*, 1988: 44. [Oral presentation during 6 July 1988.]

Gilbert, L.E. 1971. Butterfly-plant coevolution: has *Passiflora adenopoda* won the selectional race with heliconiine butterflies? *Science*, 172: 585-586.

Gilbert, L.E. 1972. Pollen feeding and the reproductive biology of *Heliconius* butterflies. *Proc. Natl. Acad. Sci. USA*, 69: 1403-1407.

Gilbert, L.E. 1979. Development of theory in the analysis of insect/plant interactions. IN: Horn, D.J., Stairs, G.R. and Mitchell, P.D., (Eds.), *Analysis of Ecological Systems*, pp. 117-154. Columbus: Ohio State University Press.

Giles, E.T. 1963. The comparative external morphology and affinities of the Dermaptera. *Trans. Roy. Entomol. Soc. London*, 115: 95-164.

Giliomee, J.H. 1961. Morphological and taxonomic studies on the males of three species of the genus *Pseudococcus* (Hemiptera: Coccoidea). *Ann. Univ. Stellenbosch*, (A), 36: 241-296.

Giliomee, J.H. 1967a. Morphology and taxonomy of adult males of the family Coccidae (Homoptera: Coccoidea). *Bull. Brit. Mus. Nat. Hist., Suppl.*, 7: 1-168.

Giliomee, J.H. 1967b. The morphology and relationships of the male of *Lecaniodiaspis elytropappi* Munting and Giliomee (Homoptera: Coccoidea). *J. Entomol. Soc. S. Africa*, 30: 185-197.

Giliomee, J.H. 1968. Morphology and relationships of the male of an *Asterolecanium* species (Homoptera: Coccoidea: Asterolecaniidae). *J. Entomol. Soc. So. Africa*, 31: 297-308.

Gillett, J.D. 1967. Natural selection and feeding speed in a blood-sucking insect. *Proc. Roy. Soc. London*, 167: 316-329.

Gillett, J.D. 1971. *Mosquitoes*. London: Weidenfeld and Nicholson. 274 p.

Gillott, C. 1980. *Entomology*. New York: Plenum Press. 729 pp.

Giudicelli, J. 1971. Monographie du genre *Thremma* (Trichoptera, Thremmatidae). *Ann. Limnol.*, 7: 125-139.

Glaser, P.W. 1927. Evidence in support of the olfactory function of the antennae of insects. *Psyche*, 34: 209-215.

Glover, P.M. 1934. The developmental stages of *Bracon tachardiae*, Cam. (Hym.). *Bull. Entomol. Res.*, 25: 521-539.

Glukhova, V.M. 1985. Morphology of male and female mouth parts of Ceratopogonidae (Diptera) and its significance in classification. IN: Skarlato, O.A., (Ed.), *Systematics of Diptera (Insecta): Ecological and Morphological Principles*, pp. 11-14. Leningrad: Academy of Sciences. [In Russian.]

Goeden, R.D. and Ricker, D.W. 1987a. Phytophagous insect faunas of the native thistles, *Cirsium brevistylum*, *Cirsium congdonii*, *Cirsium occidentale*, and *Cirsium tioganum*, in southern California. *Ann. Entomol. Soc. Am.*, 80: 152-160.

Goeden, R.D. and Ricker, D.W. 1987b. Phytophagous insect faunas of native Cirsium thistles, *C. mohavense*, *C. neomexicanum* and *C. nidulum*, in the Mojave Desert of southern California. *Ann. Entomol. Soc. Am.*, 80: 161-175.

Gohrbandt, I. 1940. Phyletische Korrelationen bei flügel-reduzierten und rüsselreduzierten Syntomiden. *Zool. Jb. (Syst.)*, 73: 313-338.

Golding, F.V. 1945. Fruit piercing Lepidoptera in Nigeria. *Bull. Entomol. Res.*, 36: 181-184.

Goldman, E.H. 1933. Comparisons of the mouth-parts of adult longhorn beetles with reference to their food (Coleoptera: Cerambycidae). *Trans. Am. Entomol. Soc.*, 59: 85-102.

Golden, H.M. 1925. Die kauenden Insektenmundteile und ihre Beziehung zur Nahrung. *Arch. Naturges.*, 7: 1-47.

Gomez-Pallerola, J.E. 1979. Un ave y otras especies nuevas de la biofacies Santa Maria de Meya (Lérida). *Bol. Geol. Min. España*, **90**: 333-346.

Gomez-Pallerola, J.E. 1986. Nuevos insectos fósiles de las calizas litográficas del Cretácico Inferior del Montsec (Lérida). *Bol. Geol. Min. España*, **97**: 717-736.

Goodchild, A.J.P. 1966. Evolution of the alimentary canal in the Hemiptera. *Biol. Rev.*, 41: 97-140.

Goodman, L.J. 1970. The structure and function of the insect dorsal ocellus. *Adv. Insect Physiol.*, 7: 97-195.

Gordon, R.M. and Crewe, M. 1953. The deposition of the infective stage of Loa loa by *Chrysops silacea*, and the early stages of its migration to the deeper dissues of the mammalian host. *Ann. Trop. Med. Parasit.*, 47: 74-85.

Gordon, R.M., Crewe, W. and Willett, K.C. 1956. Studies on the deposition, migration, and development to the blood forms of trypanosomes belonging to the *Trypanosoma brucei* Group. 1. An account of the process of feeding adopted by the tsetse-fly when obtaining a blood-meal from the mammalian host, with special reference to the ejection of saliva and the relationship of the feeding process to the deposition of the metacyclic trypanosomes. *Ann. Trop. Med. Parasitol.*, 50: 426-437.

Gordon, R.M. and Lumsden, W.H.R. 1939. The study of the behavior of the mouthparts of mosquitoes when taking up blood from living tissue together with some observations on the ingestion of microfilaria. *Ann. Trop. Med. Parasitol.*, 33: 259-278.

Gorochov, A.V. 1985. Mesozoic circkets (Orthoptera, Grylloidea) of Asia. *Paleontol. J.*, **19**: 56-66.

Gorochov, A.V. 1988. Orthopteran tegmina of the Hagloidea (Orthoptera) from the Lower Cretaceous and Jurassic. *Paleontol. J.*, **1988**: 54-66.

Goto, H.E. 1972. On the structure and function of the mouthparts of the soil-inhabiting collembolan *Folsomia candida*. *Biol. J. Linn. Soc.*, 4: 147-168.

Gottsberger, G. 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Plant Syst. Evol., Suppl.*, 1: 211-216.

Gottsberger, G. 1988. The reproductive biology of primitive angiosperms. *Taxon*, 37: 630-643.

Gotwald, W.H., Jr. 1969. Comparative morphological studies of the ants, with particular reference to the mouthparts (Hymenoptera: Formicidae). *Cornell Univ. Agr. Expt. Sta. Mem.*, **408**: 1-150.

Gotwald, W.H., Jr. 1973. Mouthpart morphology of the African ant *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae). *J. New York Entomol. Soc.*, **81**: 72-78.

Gouin, F.J. 1949. Recherches sur la morphologie de l'appareil buccal des Diptères. *Mem. Mus. Natl. Hist. Nat.*, **28**: 169-269.

Gouin, F.J. 1957. Etudes sur l'anatomie de la tête larvaire de quelques Chironomidae (Dipt., Nematoc.). I. Les structures chironomines. *Ann. Soc. Entomol. France*, **126**: 105-138.

Gouin, F.J. 1958. L'appareil buccal de *Chrysochroma bipunctatum* Scop. (Dipt. Stratiom.). *Proc. Tenth Int. Congr. Entomol.*, **1**: 517-519.

Gouin, F.J. 1959. Morphology of the larval head of some Chironomidae (Diptera, Nematocera). *Smithson. Misc. Collns.*, **137**: 175-201.

Gouin, F.J. 1968. Morphologie, Histologie und Entwicklungsgeschichte der Insekten und der Myriapoden. IV. Die Strukturen des Kopfes. *Fortschr. Zool.*, **19**: 194-282.

Graham-Smith, G.S. 1911. Some observations on the anatomy and function of the oral sucker of the blow-fly (*Calliphora erythrocephala*). *J. Hyg.*, **11**: 390-408, pls. 4-8.

Graham-Smith, G.S. 1930a. Further observations on the anatomy and function of the proboscis of the blow-fly, *Calliphora erythrocephala* L. *Parasitology*, **22**: 47-115.

Graham-Smith, G.S. 1930b. The Oscinidae (Diptera) as vectors of conjunctivitis, and the anatomy of their mouth parts. *Parasitology*, **22**: 457-467.

Grande, L. 1980. Paleontology of the Green River Formation, with a review of the fish fauna. *Bull. Geol. Surv. Wyoming*, **63**: 1-333.

Grandi, G. 1924a. Studi sullo sviluppo postembrionale delle varie razze del *Bombyx mori* L. *Boll. Lab. Zool. Gen. Agr. Portici*, **27**: 3-40.

Grandi, G. 1924b. *Neosycophila omeomorpha* Grnd. e sua importanza biologica. *Boll. Lab. Zool. Gen. Agr. Portici*, **27**: 108-130.

Grandi, G. 1925. Agaonini e Sycophagini olartici e indomalesi. *Boll. Lab. Zool. Gen. Agr. Portici*, **28**: 3-31.

Grandi,; G. 1926. Contributi alla conoscenza della biologia e della morfologia degli imenotteri melliferi e predatori. *Boll. Lab. Zool. Gen. Agr. Portici*, 29: 269-326.

Grandi, G. 1936. Morfologia ed etologia comparate di insetti a regime specializzado. XII. *Macrosiagon ferrungineum flabellatum* F. *Boll. Entomol. Bologna*, 9: 33-64.

Grandi, G. 1937. L'ipermetabolia dei ripiforidi. *Mem. Accad. Sci. Ist. Bologna*, 4: 47-57, pls. 1-2.

Grandi, G. 1959. The problems of "morphological adaptation" in insects. *Smithson. Misc. Collns.*, 137: 203-230.

Grandori, R. 1911. Contributo all'embriologia e alla biologia dell' *Apanteles glomeratus* (L.) Reinh. (Imenottero Parassita del bruco di *Pieris brassicae* L). *Redia*, 7: 363-427, pls. 13-16.

Grant, V. 1983. The systematic and geographical distribution of hawkmoth flowers in the temperate North American flora. *Bot. Gaz.*, 144: 439-449.

Grant, V. and Grant, K.A. 1983. Behavior of hawkmoths on flowers of *Datura meteloides*. *Bot. Gaz.*, 144: 280-284.

Green, E.E. 1926. On some new genera and species of Coccidae. *Bull. Entomol. Res.*, 17: 55-65.

Greene, C.T. 1926. Descriptions of larvae and pupae of two-winged flies belonging to the family Leptidae. *Proc. U.S. Natl. Mus.*, 70: 1-20, pls. 1-3.

Greene, C.T. 1929. Characters of the larvae and pupae of certain fruit flies. *J. Agr. Res.*, 38: 489-503.

Greenslade, P.J.M. 1988. Reply to R.A. Crowson's "Comments on Insecta of the Rhynie Chert" (1985 Entomol. Gen. 11(1/2): 097-098). *Entomol. Gen.*, 13: 115-117.

Greenslade, P.J.M. and Whalley, P.E.S. 1986. The systematic position of *Rhyniella praecursor* Hirst & Maulik (Collembola), the earliest known hexapod. *Second Int. Sem. Apterygota*, pp. 319-323.

Grenier, P. 1959. Remarques concernant le fonctionnement des mandibules chez les femelles de dipteres hematophages nematoceres et brachyceres. *Ann. Parasitol. Hum. Comp.*, 34: 565-585.

Grieve, E.G. 1937. The muscles of the head stomodeum of an odonate nymph, *Ischnura verticalis*. *Can. Entomol.*, 69: 211-218.

Griffiths, D. 1980. The feeding biology of ant-lion larvae: prey capture, handling and utilization. *J. Anim. Ecol.*, 49: 99-125.

Griffiths, R.B. and Gordon, R.M. 1952. An apparatus which enables the process of feeding by mosquitoes to be observed in the tissues of a live rodent, together with an account of the ejection of saliva and its significance in malaria. *Ann. Trop. Med. Parasitol.*, 46: 311-319.

Grimaldi, D.A. 1987. Amber fossil Drosophilidae (Diptera), with particular reference to the Hispaniolan taxa. *Am. Mus. Novit.*, 2880: 1-23.

Grimaldi, D.A. 1988a. Bee flies and bluets: *Bombylius* (Diptera: Bombyliidae) flower-constant on the distylous species, *Hedyotis caerulea* (Rubiaceae), and the manner of foraging. *J. Nat. Hist.*, 22: 1-10.

Grimaldi, D.A. 1988b. Still life with flowers. *Nat. Hist.*, 97: 86-89.

Grimaldi, D.A., Beck, C.W. and Boon, J.J. 1989. Occurrence, chemical characteristics, and paleontology of the fossil resins from New Jersey. *Am. Mus. Novit.*, 2948: 1-28.

Grimes, L.R. and Neunzig, H.H. 1986a. Morphological survey of the maxillae in last stage larvae of the Suborder Ditrysia (Lepidoptera): palpi. *Ann. Entomol. Soc. Am.* 79: 491-509.

Grimes, L.R. and Neunzig, H.H. 1986b. Morphological survey of the maxillae in last-stage larvae of the Suborder Ditrysia (Lepidoptera): mesal lobes (laciniogaleae). *Ann. Entomol. Soc. Am.*, 79: 510-526.

Grinfel'd, E.K. 1955. Diptera feeding on nectar and pollen and their role in the pollination of plants. *Vest. Leningrad Univ.*, 10: 15-25. [In Russian.]

Grinfel'd, E.K. 1959a. Feeding of thrips on the pollen of flowers and the origin of asymmetry in their mouthparts. *Entomol. Rev.*, 38: 715-720.

Grinfel'd, E.K. 1959b. The importance of nocturnal insects in sunflower pollination. *Agrobiologia*, 4: 634-635. [In Russian.]

Grinfel'd, E.K. 1961. The origin of the aphid/ant symbiosis. *Vest. Leningrad Univ.*, 15: 73-84 [In Russian, with English summary.]

Grinfel'd, E.K. 1973. Anthophilous evolution of the Apoidea. *Vest. Leningrad Univ., Ser. Biol.*, 28: 7-15. [In Russian, with English summary].

Grinfel'd, E.K. 1975. Anthophily in beetles (Coleoptera) and a critical evaluation of the cantharophilous hypothesis. *Entomol. Rev.*, 54: 18-22.

Grogan, W.L., Jr. and Szadziewski, R. 1988. A new biting midge from Upper Cretaceous (Cenomanian) amber of New Jersey (Diptera: Ceratopogonidae). *J. Paleontol.*, 62: 808-812.

Grove, A.J. 1919. The anatomy of the head and mouth parts of *Psylla mali*, the apple sucker, with some remarks on the function of the labium. *Parasitology*, 11: 456-488.

Gurney, A.B. 1943. A synopsis of the psocids of the tribe Psyllipsocini, including the description of an unusual new genus from Arizona (Corrodentia: Empheriidae: Empheriinae). *Ann. Entomol. Soc. Am.*, 34: 195-220.

Gurney, A.B. 1947. Notes on Dilaridae and Berothidae, with special reference to the immature stages of the Nearctic genera (Neuroptera). *Psyche*, 54: 145-169.

Gurney, A.B. 1950. On *Dicranostomus*, a remarkable Peruvian genus of katydids; and notes on other insects having elongate mandibles. *Ann. Entomol. Soc. Am.*, 43: 546-554.

Gurney, A.B. 1953. Notes on the biology and immature stages of a cricket parasite of the genus *Rhopalosoma*. *Proc. U.S. Natl. Mus.*, 103(3313): 19-34.

Gurney, A.B. and Liebermann, J. 1963. Grasshoppers of the tribe Ommexechini: a key to genera, a new Argentine genus, and notes on others (Orthoptera, Acrididae). *Proc. Biol. Soc. Washington*, 76: 127-138.

Guthörl, P. 1934. Die Arthropoden aus dem Carbon und Perm des Saar-Nahe-Pfalz-Gebietes. *Abh. Presuss. Geol. Landes.*, N.F., 164: 1-219, pls. 1-30.

Guthörl, P. 1965. Zur Arthropoden-fauna des Karbons und Perms. 21. *Protereisma rossenrakyensis* n.sp., ein Ephemeropterenfund (Insecta) aus dem niederrheinischen zechstein. *Paläont. Z.*, 39: 229-233.

Habu, A. 1962. *Fauna Japonica. Chalcidae, Leucospididae and Podagrionidae (Insecta Hymenoptera).* Tokyo: Biogeographical Society of Japan. 232 p., 19 pls.

Hadden, F.C. 1927. A check-list of insects eaten by the mantis *Paratenodera sinensis*. *Proc. Hawaiian Entomol. Soc.*, 6: 385-386.

Hagen, H.A. 1954. Uber die Neuropteren der Bernsteinfauna. *Verh. Zool. Bot. Ver. Wein*, 4: 221-232.

Hagen, H.A. 1855. *Ascalaphus proavus* aus der Rheinischen Braunkohle. *Palaeontographica*, 5: 125-126.

Hagen, H.A. 1862. Ueber die Neuroptern aus dem lithographischen Schiefer in Bayern. *Palaeontographica*, 10: 96-145.

Hagen, H.A. 1881. On the proboscis of *Nemognatha*. *Proc. Boston Soc. Hat. Hist.*, 20: 429-430.

Hagen, H.A. 1882a. Fossil insects of the Dakota Group. *Nature*, 25: 265-266.

Hagen, H.A. 1882b. Uber Psociden im Bernstein. *Stett. Entomol. Ztg.*, 43: 217-237.

Hagen, K.S. 1987. Nutritional ecology of terrestrial insect predators. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 533-577. New York: John Wiley and Sons.

Hagen, R.H. and Chabot, J.F. 1986. Leaf anatomy of maples (*Acer*) and host use by Lepidoptera larvae. *Oikos*, 47: 335-345.

Hajek, A.E. and Dahlsten, D.L. 1986. Coexistence of three species of leaf-feeding aphids (Homoptera) on *Betula pendula*. *Oecologia*, 68: 380-386.

Hakim, Z.M. 1964. Comparative anatomy of the head capsules of adult Odonata. *Ann. Entomol. Soc. Am.*, 57: 267-278.

Halffter, G. and Matthews, E.G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomol. Mexicana*, 12/14: 1-322.

Halffter, G. and Edmonds, W.D. 1982. *The Nesting Behaviour of Dung Beetles (Scarabaeinae)*. Mexico City: Instituto de Ecologia.

Hall, J.C. 1981. Bombyliidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 589-602.

Hamilton, A. 1931. The morphology of the water-scorpion, *Nepa cinera* Linn. (Rhynchota, Heteroptera). *Proc. Zool. Soc. London*, 1931: 1067-1137.

Hamilton, K.G.A. 1981. Morphology and evolution of the rhynchotan head (Insecta: Hemiptera, Homoptera). *Can. Entomol.*, **113**: 953-973.

Hamilton, W.D. 1978. Evolution and diversity under bark. *Symp. Roy. Entomol. Soc. London*, **9**: 154-175.

Hammond, A. 1874. The mouth of the crane-fly. *Hardwicke's Sci. Gossip*, **1874**: 155-160.

Handlirsch, A. 1908. *Die Fossilen Insekten und die Phylogenie der Rezenten Formen. Ein Handbuch für Paläontologen und Zoologen.* Leipzig: Engelmann. 1430 pp.

Handlirsch, A. 1911. New Paleozoic insects from the vicinity of Mazon Creek, Illinois. *Am. J. Sci.*, **31**: 297-377.

Handlirsch, A. 1918. Fossile Ephemeridenlarven aus dem Buntsandstein der Vogesen. *Verh. Zool. Bot. Ges. Wien*, **1918**: 112-114.

Handlirsch, A. 1925. *Handbuch der Entomologie*, vol. 3. Jena: Gustav Fischer. 1202 pp.

Handlirsch, A. 1937. Neue Untersuchungen über die fossilen Insekten. I. *Ann. Naturhist. Mus. Wien*, **48**: 1-140.

Handlirsch, A. 1939. Neue Untersuchungen über die fossilen Insekten. II. *Ann. Naturhist. Mus. Wien*, **49**: 1-240.

Handschin, E. 1926a. Die Collembolen des baltischen Bernsteins. *Zool. Anz.*, **65**: 179-182.

Handschin, E. 1926b. Revision der Collembolen des baltischen Bernsteins. *Entomol. Mitt.*, **15**: 161-185, 211-223, 330-342.

Handschin, E. 1926c. Uber Bernsteincollembolen. Ein Beitrag zur ökologischen Tiergeographie. *Revue Suisse Zool.*, **33**: 375-378.

Handschin, E. 1929. Ein neuer russeltypus bei einem kafer. Biologische und morphologische biobachtungen an *Leptopalpus rostratus* F. *Z. Morphol. Okol. Tiere*, **14**: 513-521.

Hannemann, H.J. 1956. Die Kopfmuskulatur von *Micropteryx calthella* (L.) (Lep.). Morphologie und Funktion. *Zool. Jb. (Anat.)*, **75**: 177-206.

Hansen, H.J. 1893a. Zur Morphologie der Gliedmaisen und Mundtheile bei Crustaceen und Insecten. *Zool. Anz.*, **16**: 193-198.

Hansen, H.J. 1893b. A contribution to the morphology of the limbs and mouth-parts of crustaceans and insects. *Ann. Mag. Nat. Hist.*, (6), 12: 417-434.

Hansen, H.J. 1894. Contributions to the knowledge of the insect fauna of Camerun. 3. On the structure and habits of *Hemimerus talpoides* Walk. *Entomol. Tidsk.*, 1894: 65-93.

Hansen, H.J. 1903. The mouth-parts of *Glossina* and *Stomoxys*. IN: Austen, E.E., (Ed.), *A Monograph of the Tse-Tse Flies*, pp. 105-120. London.

Hanski, I. 1987. Nutritional ecology of dung- and carrion-feeding insects. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 837-884. New York: John Wiley and Sons.

Harbach, R.E. 1977. Comparative and functional morphology of the mandibles of some fourth stage mosquito larvae (Diptera: Culicidae). *Zoomorphologie*, 87: 217-236.

Harbach, R.E. 1978. Comparative structure of the labio-hypopharynx of fourth stage mosquito larvae (Diptera: Culicidae), with comments on larval morphology, evolution and feeding habits. *Mosq. Syst.*, 10: 327-329.

Harborne, J.B. 1977. *Introduction to Ecological Biochemistry*. London: Academic Press.

Harder, L.D. 1981. Measurement and estimation of functional proboscis length in bumblebees (Hymenoptera: Apidae). *Can. J. Zool.*, 60: 1073-1079.

Hardy, D.E. 1971. A new *Plecia* (Diptera: Bibionidae) from Mexican amber. *Univ. California Publ. Entomol.*, 63: 65-67.

Hardy, D.E. 1981. Bibionidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 217-222.

Hare, L. 1937. Termite phylogeny as evidenced by soldier mandible development. *Ann. Entomol. Soc. Am.*, 30: 459-486.

Hargreaves, E. 1915. The life-history and habits of the greenhouse white fly (*Aleurodes vaporariorum* Westd.). *Ann. Appl. Biol.*, 1: 303-334.

Haridass, E.T. 1985. Feeding and ovipositional behaviour in some reduviids (Insecta-Heteroptera). *Proc. Indian Acad. Sci. (Animal Sci.)*, 94: 239-247.

Harland, W.B., Cox, A.V., Llewellen, P.G., Pickton, C.A.G., Smith, A.G. and Walters, R. 1982. *A Geologic Time Scale.* Cambridge: Cambridge University Press. 131 pp.

Harris, A.C. 1984. New Zealand pre-Pleistocene insect fossils. *New Zealand Entomol.*, **8**: 47-49.

Hartland-Rowe, R. 1953. Feeding mechanism of an Ephemeropteran nymph. *Nature*, **172**: 1109-1110.

Hartley, J.C. 1963. The cephalopharyngeal apparatus of syrphid larvae and its relationship to other Diptera. *Proc. Zool. Soc. London*, **141**: 261-280.

Hasenfuss, I. 1969. Zur homologie der Borstenmusterelemente der Larven-Kopfkapsel einiger monotrysischer Lepidoptera. *Beitr. Entomol.*, **19**: 289-301.

Hassanein, M.H. and Abd El-Salam, A.L. 1962. Studies on the morphology of the bee louse, *Braula coeca* Nitzsch. *Bull. Soc. Entomol. Egypte*, **46**: 45-59.

Hasterud, H.D. 1974. Pollination of some Ericaceae in Norway. *Norwegian J. Bot.*, 21: 211-216.

Hata, K. and Edmonds, W.D. 1983. Structure and function of the mandibles of adult dung beetles (Coleoptera: Scarabeidae). *Int. J. Insect Morphol. Embryol.*, **12**: 1-12.

Hatch, M.H. 1927. A revision of fossil Gyrinidae. *Bull. Brooklyn Entomol. Soc.*, 22: 89-96.

Haub, F. 1967. Der Kopf von *Pseudomenopon pilosum* (Scopoli) (Mallophaga-Amblycera). *Zool. Jb. (Anat.)*, **84**: 493-558.

Haughton, S.H. 1924. The fauna and stratigraphy of the Stormberg Series. *Ann. So. Afr. Mus.*, 12: 323-495.

Haupt, H. 1950. Die käfer (Coleoptera) aus der Eozanen braunkohle des Geiseltales. *Geologica*, **6**: 1-168.

Haviland, M.D. 1921. On the bionomics and development of *Lygocerus testaceimanus*, Kieffer, and *Lygocerus cameroni*, Kieffer (Proctotrypoidea-Ceraphronidae), parasites of *Aphidius* Braconidae). *Quart. J. Micros. Sci.*, N.S., **65**: 101-127.

Hawkins, C.P. and MacMahon, J.A. 1989. Guilds: the multiple meanings of a concept. *Ann. Rev. Entomol.*, 34: 423-451.

Hayes, W.P. 1928. The epipharynx of lamellicorn larvae (Coleop.), with a key to common genera. *Ann. Entomol. Soc. Am.*, 21: 282-306.

Heath, J., 1959. The food plants of adult micropterygids. *Entomol. Mon. Mag.*, 95: 188.

Hebard, M. 1928. The group Luzarae of the subfamily Phylangopsinae (Orthoptera, Gryllidae). *Trans. Am. Entomol. Soc.*, 54: 1-56.

Heddergott, H. 1938. Kopf und Vorderdarm von *Panorpa communis* L. *Zool. Jb. (Anat.)*, 64: 229-294.

Hedquist, K.-J. 1967. Notes on Megalyrridae (Hym., Ichneumonoidea) and description of new species from Madagascar. *Ann. Soc. Entomol. France*, N.S., 3: 239-246.

Heer, O. 1847. Die Insektenfauna der Tertiargebilde von Oeningen und von Radoboj in Croatien. Teil 1: Käfer. *Neue Denkschr. Allg. Schweiz. Ges. Naturwiss.*, 8: 1-228, pls. 1-8.

Heer, O. 1849. Die Insekten fauna der Teriärgebilde von Oeningen und von Radoboj in Croatien. Teil 2: Heuschren, Florfliegen, Aderflügler, Schmetterlinge, und Fliegen. *Neue Denkschr. Allg. Schweiz. Ges. Naturwiss.*, 9: 1-265, pls. 1-17.

Heer, O. 1856. Uever die fossilen insekten von Aix-en-Provence. Vierteljahreschr. *Naturfor. Ges.*, 1: 1-40.

Heer, O. 1865. Fossile Hymenopteren aus Oeningen und Radoboj. *Neue Denkschr. Allg. Schweiz Ges. Naturwiss.*, 22: 1-42, pls. 1-3.

Heie, O.E. 1967. Studies of fossil aphids (Homoptera: Aphidoidea). *Spoilia Zool. Mus. Haun.*, 26: 1-274.

Heie, O.E. 1985. Fossil aphids: a catalogue of fossil aphids, with comments on systematics and evolution. *Proc. Int. Aphidiological Symp.*, pp. 101-134. Warsaw: Polish Academy of Sciences.

Heinrich, C. 1918. On the lepidopterous genus *Opostega* and its larval affinities. *Proc. Entomol. Soc. Washington*, 20: 27-34.

Heithaus, R. 1983. *Bombus epihippiatus* (chiquiza de montaña, bumblebee). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 700-701. Chicago: University of Chicago Press.

Heming, B.S. 1978. Structure and function of the mouthparts in larvae of *Haplothrips verbasci* (Osborn) (Thysanoptera, Tubulifera, Phlaeothripidae). *J. Morphol.*, 156: 1-37.

Hendrix, S.D. 1980. An evolutionary and ecological perspective of the insect fauna of ferns. *Am. Nat.*, 115: 171-196.

Hengeveld, R. 1980a. Qualitative and quantitative aspects of the food of ground beetles (Coleoptera, Carabidae): a review. *Neth. J. Zool.*, 30: 555-563.

Hengeveld, R. 1980b. Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera, Carabidae). *Neth. J. Zool.*, 30: 564-584.

Hengeveld, R. 1980c. Food specialization in ground beetles: An ecological or a phylogenetic process? *Neth. J. Zool.*, 30: 585-594.

Hengeveld, R. 1981. The evolutionary relevance of feeding habits of ground beetles (Coleoptera: Carabidae). *Entomol. Scand., Suppl.*, 15: 305-315.

Hennig, W. 1935. Der Filterapparat im Pharynx der Cyclorrhaphen-larven und die biologische Deutung der Madenform. *Zool. Anz.*, 111: 131-139.

Hennig, W. 1948. *Die Larvenformen der Dipteren.* Volume 1. Berlin: Akademie-Verlag. 185 pp.

Hennig, W. 1950. *Die Larvenformen der Dipteren.* Volume 2. Berlin: Akademie-Verlag. 458 pp.

Hennig, W. 1952. *Die Larvenformen der Dipteren.* Volume 3. Berlin: Akademie-Verlag. 628 pp.

Hennig, W. 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. *Beitr. Entomol.*, 3: 1-85.

Hennig, W. 1956. Beitrag zur Kenntnis der Milichiiden-Larven. *Beitr. Entomol.*, 6: 138-145.

Hennig, W. 1964. Die Dipteren-Familie Sciadoceridae im Baltischen Bernstein (Diptera: Cyclorrhapha Aschiza). *Stutt. Beitr. Naturk.*, (B), 127: 1-10.

Hennig, W. 1965. Die Acalyptratae des Baltischen Bernsteins. *Stutt. Beitr. Naturk.*, (B), 145: 1-215.

Hennig, W. 1966. Dixidae aus dem Baltischen Bernsteins, mit Bemerkungen über einige andere fossile Arten aus der Gruppe Culicoidea (Diptera Nematocera). *Stutt. Beitr. Naturk.*, (B), 153: 1-16.

Hennig, W. 1967a. Die sogenannten "niederen Brachycera" im Baltischen Bernstein (Diptera: Fam. Xylophagidae, Xylomyiidae, Rhagionidae, Tabanidae). *Stutt. Beitr. Naturk.*, (B), **174**: 1-51.

Hennig, W. 1967b. Neue Acalyptratae aus dem Baltischen Bernstein (Diptera: Cyclorrhapha). *Stutt. Beitr. Naturk.*, (B), **175**: 1-27.

Hennig, W. 1967c. Therevidae aus dem Baltischen Bernstein mit einigen Bermerkungen über Asilidae und Bombyliidae (Diptera Brachycera). *Stutt. Beitr. Naturk.*, (B), **176**: 1-14.

Hennig, W. 1968. Ein weiterer Vertreter der Familie Acroceridae im Baltischen Bernstein (Diptera: Brachycera). *Stutt. Beitr. Naturk.*, **185**: 1-6.

Hennig, W. 1969. Neue Ubersicht über die aus dem Baltischen bekannten Acalyptratae. *Stutt. Beitr. Naturk.*, **209**: 1-42.

Hennig, W. 1970. Insektenfossilien aus der unteren Kreide. II. Empididae (Diptera, Brachycera). *Stutt. Beitr. Naturk.*, **214**: 1-12.

Hennig, W. 1971a. Insektenfossilien aus der unteren Kreide. III. Empidiformia ("Microphorinae") aus der unteren Kreide und aus dem Baltischen Bernstein: ein Vertreter der Cychorrhapha aus dem unteren Kreide. *Stutt. Beitr. Naturk.*, (B), **232**: 1-28.

Hennig, W. 1971b. Die Familien Pseudopomyzidae und Milichidae im baltischen Bernstein (Diptera: Cyclorrhapha). *Stutt. Beitr. Naturk.*, **233**: 1-16.

Hennig, W. 1972a. Beiträge zur Kenntnis der rezenten und fossilen Carnidae, mit besonderer Berücksichtigung einer neuen Gattung aus Chile (Diptera: Cyclorrhapha). *Stutt. Beitr. Naturk.*, (B), **240**: 1-20.

Hennig, W. 1972b. Insektenfossilien aus der unteren Kreide. IV. Psychodidae (Phlebotominae), mit einer kritischen Ubersicht über das phylogenetische System der Familie und die bisher beschreibenen Fossilien (Diptera). *Stutt. Beitr. Naturk.*, (B), **241**: 1-69.

Hennig, W. 1981. *Insect Phylogeny*. New York: John Wiley and Sons. 514 pp.

Henry, C.S. 1982. Neuroptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 470-482. New York: McGraw-Hill Book Co.

Henson, H. 1950. On the head capsule and mouth parts of *Forficula auricularia* Linn. (Dermaptera). *Proc. Roy. Soc. London*, (A), **25**: 10-18.

Hepburn, H.R. 1969. The skeleto-muscular system of Mecoptera: the head. *Univ. Kansas Sci. Bull.*, **48**: 721-765.

Hepburn, H.R. 1971. Proboscis extension and recoil in Lepidoptera. *J. Insect Physiol.*, **17**: 637-656.

Hering, E.M. 1951. *Biology of the Leaf Miners.* The Hague: W. Junk, Publishers. 420 pp.

Hering, E.M. 1954. *Bestimmungstabellen der Blattminen von Europa.* Volumes 1,2. The Hague: W. Junk, Publishers. 1185 pp.

Hermann H.R., Hunt, A.N. and Buren, W.F. 1971. Mandibular groove in *Polistes annularis* (L.) and *Vespula maculata* (L.) (Hymenoptera: Vespidae). *Int. J. Insect Morphol. Embryol.*, **1**: 43-49.

Herrera, C.M. 1982. Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions. *Am. Nat.*, **120**: 218-241.

Herrera, C.M. 1988. Variation in mutualisms: the spatiotemporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.*, **35**: 95-125.

Herriot, A.D. 1934. The renewal and replacement of the styles of sucking insects during each stadium and the method of penetration. *Can. J. Res.*, **11**: 602-612.

Hetrick, L.A. 1935. The morphology of the head of the scorpionfly. *Proc. Louisiana Acad Sci.*, **2**: 113-120.

Hewitt, C.G. 1907. The structure, development and bionomics of the house-fly, *Musca domestica*, Linn. Part 1. Anatomy of the fly. *Quart. J. Micros. Soc.*, **51**: 395-448, pls. 22-26.

Heyden, C. von 1962. Braunkohle des Niederrfhein's der Wetterau und der Röhn. *Palaeontographica*, **10**: 62-82, pl. 10.

Hickey, L.J. and Doyle, J.A. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev.*, **43**: 3-104.

Hickey, L.J. and Hodges, R.W. 1975. Lepidopteran leaf mine from the Early Eocene Wind River Formation of northeastern Wyoming. *Science*, **189**: 718-720.

Hickin, N.E. 1968. *Caddis Larvae: Larvae of the British Trichoptera.* Rutherford, England: Fairleigh Dickinson University Press. 480 p.

Hijii, N. 1983. Arboreal arthropod fauna in a forest. I. Preliminary observation on seasonal fluctuations in density, biomass, and faunal composition in a *Chamaecyparis obtusa* plantation. *Jap. J. Ecol.*, 33: 435-444.

Hijii, N. 1984. Arboreal arthropod fauna in a forest. II. Presumed community structures based on biomass and number of arthropods in a *Chamaecyparis obtusa* plantation. *Jap. J. Ecol.*, 34: 187-193.

Hijii, N. 1986. Density, biomass, and guild structure of arboreal arthropods as related to their inhabited tree size in a *Cryptomeria japonica* plantation. *Ecol. Res.*, 1: 97-118.

Hill, C.C. and Emery, W.T. 1937. The biology of *Platygaster herrickii*, a parasite of the hessian fly. *J. Agr. Res.*, 55: 199-213.

Hill, D.S. 1983. *Agricultural Insect Pests of the Tropics and Their Control*, 2nd edn. Cambridge: Cambridge University Press. 746 p.

Hinton, H.E. 1943. The larvae of the Lepidoptera associated with stored products. *Bull. Entomol. Res.*, 34: 163-212.

Hinton, H.E. 1947. The dorsal cranial areas of caterpillars. *Ann. Mag. Nat. Hist.*, (11), 14: 843-852.

Hinton, H.E. 1957. The larvae of the species of Tineidae of economic importance. *Bull. Entomol. Res.*, 47: 251-346.

Hinton, H.E. 1963. The ventral ecdysial lines of the head of endopterygote larvae. *Trans. Roy. Entomol. Soc. London*, 115: 39-61.

Hinton, H.E. 1977. Enabling mechanisms. *Proc. 15th Int. Congr. Entomol.*, pp. 71-83.

Hirsch, F. 1986. Die Mundwerkzeuge von *Phthirus pubis* L. (Anoplura). *Zool. Jb. (Anat.)*, 114: 167-204.

Hirst, S. and Maulik, S. 1926. On some arthropod remains from the Rhynie Chert (Old Red Sandstone). *Geol. Mag.*, 63: 69-71.

Hiznay, P.A. and Krause, J.B. 1955. The structure and musculature of the larval head and mouthparts of the horned passalus beetle, *Popilius disjunctus* Illiger. *J. Morphol.*, 97: 55-75.

Hobby, B.M. 1934. Notes on predaceous Anthomyiidae and Cordyluridae. *Entomol. Mon. Mag.*, 70: 185-190.

Hobby, B.M. and Killington, F.J. 1934. The feeding habits of British Mecoptera; with a synopsis of the British species. *Trans. Soc. Brit. Entomol.*, 1: 39-49.

Hocking, B. 1971. Blood-sucking behavior of terrestrial arthropods. *Ann. Rev. Entomol.*, **16**: 1-26.

Hocking, B. 1980. Ant-plant mutualism: evolution and energy. IN: Gilbert, L.E. and Raven, P.H., (Eds.), *Coevolution of Animals and Plants*, rev. edn., pp. 78-90. Austin: University of Texas Press.

Hodek, I. 1973. *Biology of the Coccinellidae.* The Hague: W. Junk, Publishers. 260 pp.

Hodges, R.W. 1962. A revision of the Cosmopterigidae of America north of Mexico, with a definition of the Momphidae and Walshiidae (Lepidoptera: Glechioidea). *Entomol. Am.*, N.S., 42: 1-171.

Hodkinson, I.D. 1973. The immature stages of *Ptychoptera lenis lenis* (Diptera: Ptychopteridae) with notes on their biology. *Can. Entomol.*, 105: 1091-1099.

Hodkinson, I.D. 1985. Co-evolution between psyllids (Homoptera: Psylloidea) and rain-forest trees: the first 120 million years. IN: Chadwick, A.C. and Sutton, S., (Eds.), *Tropical Rain Forest: The Leeds Symposium*, pp. 187-194. Leeds: Leeds Philosophical Society.

Hodkinson, I.D. 1989. The biogeography of the Neotropical jumping plant-lice (Insecta: Homoptera: Psylloidea). *J. Biogeogr.*, 16: 203-217.

Hoffman, A.D. 1932. Miocene insect gall impressions. *Bot. Gaz.*, 93: 341-342.

Hoffmann, R.W. 1905. Uber die Morphologie und die Funktion der Kauwerkzeuge von *Tomocerus plumbeus* L. II. Beitrag zur Kenntnis der Collembolen. *Z. Wiss. Zool.*, **82**: 638-663.

Hoffmann, R.W. 1908. Uber die Morphologie und die Funktion der Kauwerkzeuge und uber das Kopfnervensystem von *Tomocerus plumbeus* L. *Z. Wiss. Zool.*, 89: 598-689.

Hoffmann, R.W. 1911. Zur Kenntnis der Entwicklukngsgeschichte der Collembolen. *Zool. Anz.*, 38: 353-377.

Hogue, C.L. 1981. Blephariceridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 191-198.

Hogue, C.L. 1983. Culicoides (purrujas, biting midges, punkies, no-see-ums). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, p. 713. Chicago: University of Chicago Press.

Hoke, G. 1924. The anatomy of the head and mouthparts of Plecoptera. *J. Morphol.*, **38**: 347-373.

Holling, C.S. 1961. Principles of insect predation. *Ann. Rev. Entomol.*, **6**: 163-182.

Holloway, B.A. 1972. The systematic position of the genus *Diphyllostoma* Fall. (Coleoptera: Scarabaeoidea). *New Zealand J. Sci.*, **15**: 31-38.

Holloway, B.A. 1976a. A new bat-fly family from New Zealand (Diptera: Mystacinobiidae). *New Zealand J. Zool.*, **3**: 279-301.

Holloway, B.A. 1976b. Pollen-feeding in hover-flies (Diptera: Syrphidae). *New Zealand J. Zool.*, **3**: 339-350.

Holloway, J.D., Bradley, J.D., Carter, D.J. and Betts, C.R., (Eds.). 1987. *Guides to Insects of Importance to Man. No. 1. Lepidoptera*. London: CAB International.

Holmgren, N. 1904a. Zur Morphologie des Insektenkopfes. *Z. Wiss. Zool.*, **76**: 343-355.

Holmgren, N. 1904b. Zur Morphologie des Insektenkopfes. 1. Zum metameren Aufbau des Kopfes der *Chironomus* larve. *Z. Wiss. Zool.*, **76**: 439-477.

Holmgren, N. 1909. Termitenstudien. 1. Anatomische untersuchungen. *Kungl. Svenska Vetensk. Handl.*, **44**: 1-215.

Hong, Y.-C. 1983. *Middle Jurassic Fossil Insects in North China*. Beijing: Geological Publishing House. 224 pp., pls. 1-28.

Honomichl, K. 1975. Beitrag zur Morphologie des Kopfes der Imago von *Gyrinus substriatus* Stephens, 1829 (Coleoptera, Insecta). *Zool. Jb. (Anat.)*, **94**: 218-295.

Honomichl, K. 1976. Feinstruktur eines Muskelrezeptors im Kopf von *Dermestes maculatus* DeGeer (Insecta, Coleoptera). *Zoomorphologie*, **85**: 59-71.

Honomichl, K. 1978. Feinstruktur zweier Propriorezeptoren im Kopf von *Oryzaephilus surinamensis* (L.) (Insecta, Coleoptera). *Zoomorphologie*, **90**: 213-226.

Hooke, R. 1665. *Micrographia or Some Physiological Descriptions of Minute Bodies Made by Magnifying Glasses with Observations and Inquiries There Upon.* London: Martyn and Allestry.

Hopkins, A.D. 1896. Notes on the habits of certain mycetophilids, with descriptions of *Epidapus scabiei*, sp. nov. *Proc. Entomol. Soc Washington*, 3: 149-161.

Hopkins, D.M., Matthews, J.V., Wolfe, J.A. and Silberman, M.L. 1971. A Pliocene flora and insect fauna from the Bering Strait region. *Palaeogeog., Palaeoclim., Palaeoecol.*, 9: 211-231.

Hopkins, G.H.E. and Clay, T. 1952. *A Check List of the Genera and Species of Mallophaga.* London: 362 pp.

Hopkins, G.H.E. and Traub, R. 1955. The genus *Cratynius* Jordan Siphonaptera) and its systematic position, with a description of a new species. *Trans. Roy. Entomol. Soc. London*, 107: 249-264.

Horsfield, D. 1978. Evidence for xylem feeding by *Philaenus spumarius* (L.) (Homoptera: Cercopidae). *Entomol. Exp. Appl.*, 24: 95-99.

Hosford, R.C. 1913. Segmentation of the head of insects. *Kansas Univ. Sci. Bull.*, 8: 65-72, pls. 1-4.

Howard, L.O. 1905. *The Insect Book. A Popular Account of the Bees, Wasps, Ants, Grasshoppers, Flies and Other North American Insects Exclusive of the Butterflies, Moths and Beetles, with Full Life Histories, Tables and Bibliographies.* New York: Doubleday, Page and Co. 429 pp.

Howden, H.F. 1955. Biology and taxonomy of North American beetles of the subfamily Geotrupinae with revisions of the genera *Bolbocerosoma*, *Eucanthus*, *Geotrupes* and *Peltogeotrupes* (Coleoptera). *Proc. U.S. Natl. Mus.*, 104: 151-319.

Hottes, F.C. 1954. Some observations on the rostrum of *Cinara puerca* Hottes (Aphidae). *Great Bas. Nat.*, 14: 83-86.

Hoyt, C.P. 1952. The evolution of the mouth parts of adult Diptera. *Microentomology*, 17: 61-125.

Hu, J.-S. and Peng, H.T. 1936. The morphological studies on the mouth parts of some Diptera. *Peking Nat. Hist. Bull.*, 10: 117-125, pls. 1-2.

Hubbard, M.D. and Savage, H.M. 1981. The fossil Leptophlebiidae (Ephemeroptera): a systematic and phylogenetic review. *J. Paleontol.*, 55: 810-813.

Huckett, H.C. 1987. Anthomyiidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, **28**: 1099-1114.

Huckett, H.C. and Vockeroth, J.F. 1987. Muscidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, **28**: 1115-1131.

Hudson, A. 1970. Notes on the percing mouthparts of three species of mosquitoes (Diptera: Culicidae) viewed with the scanning electron microscope. *Can. Entomol.*, **102**: 501-509.

Hudson, G.B. 1945. A study of the tentorium of some orthopteroid Hexapoda. *J. Entomol. Soc. So. Africa*, **8**: 71-90.

Hudson, G.V. 1928. *The Butterflies and Moths of New Zealand.* Wellington, New Zealand: Ferguson and Osborn. 386 pp.

Hughes, N.F. and Smart, J. 1967. Plant-insect relationships in Palaeozoic and later time. IN: Harland, W.B., et al., (Eds.), *The Fossil Record*, pp. 107-117. London: The Geological Society.

Hull, F.M. 1938. Family Syrphidae. IN: Carpenter, F.M., et al., Fossil insects from the Creede Formation, Colorado. Part 1. Introduction, Neuroptera, Isoptera and Diptera. *Psyche*, **45**: 116-117.

Hull, F.M. 1957. Tertiary flies from Colorado and the Baltic amber. *Psyche*, **64**: 37-45, pls. 1-3.

Hulley, P.E. 1988. Caterpillar attacks plant mechanical defence by mowing trichomes before feeding. *Ecol. Entomol.*, **13**: 239-241.

Hungerford, H.B. 1919. The biology and ecology of aquatic and semiaquatic Hemiptera. *Kansas Univ. Sci. Bull.*, **11**: 3-328.

Hurd, P.D., Smith, R.F. and Durham, J.W. 1962. The fossiliferous amber of Chiapas, México. *Ciencia*, **21**: 107-118.

Hutchinson, G.E. 1981. Thoughts on aquatic insects. *Bioscience*, **31**: 495-500.

Hynes, H.B.N. 1942. A study of the feeding of adult stoneflies (Plecoptera). *Proc. Roy. Soc. London*, (A), **17**: 81-82.

Hyslop, J.A. 1915. Notes on the habits and anatomy of *Horistonotus uhlerii* Horn (Coleoptera; Elateridae). *Proc. Entomol. Soc. Washington*, **17**: 179-183, pls. 20-21.

Illies, J. 1960. Archiperlaria, eine neue Unterordnung der Plecopteren. *Beit. Entomol.*, 10: 661-697.

Illies, J. 1965. Phylogeny and zoogeography of the Plecoptera. *Ann. Rev. Entomol.*, 10: 117-140.

Illies, J. 1967. Megaloptera und Plecoptera (Ins.) aus den jungpliozänen Süsswassermergein von Willershausen. *Ber. Naturhist. Ges.*, 111: 47-55.

Imms, A.D. 1907. On the larval and pupal stages of *Anopheles maculipennis*, Meigen. *J. Hyg.*, 7: 291-318.

Imms, A.D. 1911. On the life-history of *Croce filipennis* Westw. (Order Neuroptera, Fam. Hemerobiidae). *Trans. Linn. Soc. London*, (2), 11: 151-160.

Imms, A.D. 1942. On *Braula coeca* Nitsch and its affinities. *Parasitology*, 34: 88-100.

Imms, A.D. 1944. On the constitution of the maxillae and labium in Mecoptera and Diptera. *Quart. J. Micros. Sci.*, 85: 73-96.

Imms, A.D. and Chatterjee, N.C. 1915. On the structure and biology of *Tachardia lacca*, Kerr, with observations on certain insects predaceous or parasitic upon it. *Indian For. Mem.*, 3: 1-41.

Ippolito, R. 1977. Note morfo-biologiche su *Cnephasia incertana* Tr. e *Cnephasia cinareana* Chr. (Lepidoptera-Tortricidae-Cnephasiini) viventi su carciofo. *Entomologica*, 13: 121-147.

Irwin, M.E. and Lyneborg, L. 1981. Therevidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 513-524.

Isely, F.B. 1938. The relations of Texas Acrididae to plants and soils. *Ecol. Mon.*, 8: 551-604.

Isely, F.B. 1944. Correlation between mandibular morphology and food specificity in grasshoppers. *Ann. Entomol. Soc. Am.*, 37: 47-67.

Ishikawa, S. 1969. The spectral sensitivity and components of the visual system in the stemmata of silkworm larvae, *Bombyx mori* L. (Lep., Bombycidae). *Appl. Entomol. Zool.*, 4: 87-99.

Issiki, S.T. 1931. On the morphology and systematics of Micropterygidae (Lepidoptera Homoneura) of Japan and Formosa, with some considerations on the Australian, European, and North American forms. *Proc. Zool. Soc. London*, 1931: 999-1039.

Issiki, S.T. 1933. Morphological studies on the Panorpidae of Japan and adjoining conuntries and comparison with American and European forms. *Jap. J. Zool.*, 4: 315-416.

Jaboulet, M.-C. 1960. Contribution a l'etude des larves d'haliplides. *Trav. Lab. Zool., Univ. Dijon*, 31: 1-17, figs. 1-30.

Jackson, D.J. 1961. Observations on the biology of *Caraphractus cinctus* Walker (Hymenoptera: Mymaridae), a parasitoid of the eggs of Dytiscidae (Coleoptera). *Parasitology*, 51: 269-294.

Jaksic, F.M. 1981. Abuse and misuse of the term "guild" in ecological studies. *Oikos*, 37: 397-400.

James, H.C. 1928. On the life-histories and economic status of certain cynipid parasites of dipterous larvae, with descriptions of some new larval forms. *Ann. App. Biol.*, 15: 287-316.

James, M.T. 1937. A preliminary review of certain families of Diptera from the Florissant Miocene beds. *J. Paleontol.*, 11: 241-247.

James, M.T. 1971. A stratiomyid fly (Diptera) from the amber of Chiapas, Mexico. *Univ. California Publ. Entomol.*, 63: 71-73.

James, M.T. 1981a. Xylophagidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 489-492.

James, M.T. 1981b. Stratiomyidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 497-512.

James, M.T. and Harwood, R.F. 1969. The feeding apparatus of insects and Acarina. IN: James, M.T. and Harwood, R.F., *Herm's Medical Entomology*, 6th edn., pp. 24-38. London: Macmillan Co.

James, M.T. and Turner, W.J. 1981. Rhagionidae. IN: McAlpine, J.F., et al., (Ed.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 483-488.

Jamieson, B.G.M. 1987. *The Ultrastructure and Phylogeny of Insect Spermatozoa*. Cambridge: Cambridge University Press. 320 p.

Jancke, G.D. 1955. Zur Morphologie der mannlichen Cocciden. *Z. Angew. Entomol.*, 37: 265-314.

Janetschek, H. 1954. Ueber Felsenspringer der Mittelmeerländer (Thysanura, Machilidae). *Eos*, 30: 163-314.

Janetschek, H. 1955. Uber mitteleuropäische Felsenspringer (Ins., Thysanura). *Oster. Zool. Z.*, 5: 281-328.

Jaetschek, H. 1970. Ordnung Protura (Beintastler). IN: Beier, M., (Ed.), *Handbuch der Zoologie*, Band 4, Hälfte 2, Lfg. 14, Beitr. 3: 1-72.

Janvier, H. 1933. Etude biologique de quelques Hymenopteres du Chili. *Ann. Sci. Nat., Zool.*, (10), 16: 209-356.

Janzen, D.H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science*, 171: 203-205.

Janzen, D.H., ed. 1983. *Costa Rican Natural History.* Chicago: University of Chicago Press. 816 p.

Janzen, D.H. 1983. Blastophaga and other Agaonidae (avispita del higo, fig wasp). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 696-700. Chicago: University of Chicago Press.

Jarial, M.S., Scudder, G.G.E. and Teraguchi, S. 1969. Observations on the labium of Corixidae (Hemiptera). *Can. J. Zool.*, 47: 713-715.

Jarzembowski, E.A. 1976. Report of Easter Field Meeting: the Lower Tertiaries of the Isle of Wight, 27-31.III. 1975. *Tertiary Res.*, 1: 11-16.

Jarzembowski, E.A. 1980. Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. *Bull. Brit. Mus. Nat. Hist. (Geol.)*, 33: 237-293.

Jarzembowski, E.A. 1981. An Early Cretaceous termite from southern England (Isoptera: Hodotermitidae). *Syst. Entomol.*, 6: 91-96.

Jarzembowski, E.A. 1984. Early Cretaceous insects from southern England. *Mod. Geol.*, 9: 71-93.

Jarzembowski, E.A. 1986. A fossil enicocephalid bug (Insecta: Hemiptera) from the London Clay (Early Eocene) of the Isle of Sheppey, southern England. *Tertiary Res.*, 8: 1-5.

Jarzembowski, E.A. 1987. The occurrence and diversity of Coal Measure insects. *J. Geol. Soc. London*, 144: 507-511.

Jarzembowski, E.A. 1989. A fossil aphid (Insecta: Hemiptera) from the Early Cretaceous of southern England. *Cret. Res.*, 10: 239-248.

Jawlowski, H. 1936. Uber den Gehirnbau der Kafer. *Z. Morphol. Okol. Tiere*, 32: 67-91.

Jayewickreme, S.H. 1940. A comparative study of the larval morphology of leaf-mining Lepidoptera in Britain. *Trans. Roy. Entomol. Soc. London*, 90: 63-105.

Jeannel, R.G. 1949. Les insectes. Classification, et phylogénie les insectes fossiles, évolution et géonémie. IN: Grassé, P.-P., (Ed.), *Traité de Zoologie*, 9: 1-1117.

Jeannel, R.G. 1960. *Introduction to Entomology*. London: Hutchinson Scientific & Technical. 344 p.

Jeannenot, F. 1956. Contribution a l'etude des collemboles, *Deuterosminthurus quinquefasciatus*. *Trav. Lab. Zool., Univ. Dijon*, 19: 1-25, figs. 1-23.

Jell, P.A. and Duncan, P.M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Mem. Assn. Australas. Palaeontol.*, 3: 111-205.

Jepsen, G.L. 1966. Early Eocene bat from Wyoming. *Science*, 154: 1333-1336.

Jermy, T. 1985. Is there competition between phytophagous insects? *Z. Zool. Syst. Evol.-Forsch.*, 23: 275-285.

Jewett, S.G., Jr. 1956. Plecoptera. IN: Usinger, R.L., (Ed.), *Aquatic Insects of California, with Keys to North American Genera and California Species*, pp. 155-181. Berkeley: University of California Press.

Jobling, B. 1926. A comparative study of the structure of the head and mouth parts in the Hippoboscidae (Diptera Pupipara). *Parasitology*, 18: 319-349.

Jobling, B. 1928a. The structure of the head and mouth-parts in the Nycteribiidae (Diptera Pupipara). *Parasitology*, 20: 254-272.

Jobling, B. 1928b. The structure of the head and mouth parts in *Culicoides pulicaris*, L. (Diptera: Nematocera). *Bull. Entomol. Res.*, 18: 211-236.

Jobling, B. 1929. A comparative study of the structure of the head and mouth parts in the Streblidae (Diptera Pupipara). *Parasitology*, 21: 417-445.

Jobling, B. 1933. A revision of the structure of the head, mouth-part and salivary glands of *Glossina palpalis* Rob.-Desv. *Parasitology*, 24: 449-490.

Jobling, B. 1976. On the fasicle of blood-sucking Diptera. In addition a description of the maxillary glands in *Phlebotomus papatasi*, together with the musculature of the labium and pulsatory organ of both the latter species and also of some other Diptera. *J. Nat. Hist.*, **10**: 457-461.

Johannsen, O.A. 1934. Aquatic Diptera. Part I. Nematocera, exclusive of Chironomidae and Ceratopogonidae. *Mem. Cornell Univ. Agr. Exp. Sta.*, **164**: 1-71.

Johnson, L.K. 1983. *Trigona fulviventria* (abeja, atarra, abeja jicote, culo de vaca, trigona, stingless bee). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 770-772. Chicago: University of Chicago Press.

Johnson, P.T. 1957. A classification of the Siphonaptera of South America. *Mem. Entomol. Soc. Am.*, **5**: 1-299.

Johnson, W.T. and Lyon, H.H. 1976. *Insects that Feed on Trees and Shrubs*. Ithaca: Cornell University Press. 464 pp.

Jolivet, P. 1986. *Insects and Plants: Parallel Evolution and Adaptations*. New York: E.J. Brill/Flora and Fauna Publications. 197 pp.

Jones, C.J. 1989. Introduction: coevolution of hematophagous arthropods and their vertebrate hosts. IN: Jones, C.J. and Williams, R.E., (Eds.), *Physiological Interactions between Hematophagous Arthropods and Their Vertebrate Hosts*, pp. 1-3. College Park, MD: Entomological Society of America.

Jones, T. 1954. The external morphology of *Chirothrips hamatus* (Trybom) (Thysanoptera). *Trans. Roy. Entomol. Soc. London*, **105**: 163-187.

Jones, W.A. and Earle, F.R. 1966. Chemical analyses of seeds. II. Oil and protein content of 759 species. *Econ. Bot.*, **20**: 127-155.

Joossee, E.N.G. 1983. New developments in the ecology of Apterygota. *Pedobiologia*, **25**: 217-234.

Jordan, K. 1888. Anatomie und Biologie der Physapoda. *Z. Wiss. Zool.*, **47**: 541-620, pls. 36-38.

Jordan, K. 1916. On the species of *Somatobrachys* in the Tring Museum. *Novit. Zool.*, **23**: 350-358, pls. 7,8.

Jordan, K. 1923. On a sensory organ found on the head of many Lepidoptera. *Novit. Zool.*, **30**: 155-158, pl. 2.

Jordan, K. 1928. On some Lepidoptera of special interest, with remarks on morphology and nomenclature. *Novit. Zool.*, **34**: 132-146, pls. 1-3.

Jordan, K.H.C. 1953. Eine weitere fossile Notonectida (Hem. Het.) von Rott im Siebengebirge. *Zool. Anz.*, **150**: 245-249.

Kadam, K. 1961. Studies on the morphology of an Indian earwig, *Labidura riparia*, Pall., var. *inermis*, Brunner. *J. Zool. Soc. India*, 13: 34-49.

Kadic, O. 1902. Studien über das Labium der Coleoptern. *Jen. Z. Naturwiss.*, **36**: 207-228, pl. 12.

Kaiser, W. 1975. The relationship between visual movement detection and colour vision in insects. IN: Horridge, G.A., (Ed.), *The Compound Eye and Vision of Insects*, pp. 359-377. Oxford: Oxford University Press.

Kalmus, H. 1945. Correlations between flight and vision, and particularly between wings and ocelli, in insects. *Proc. Roy. Entomol. Soc. London*, **20A**: 84-96.

Kalugina, N.S. 1976. Non-biting midges of the subfamily Diamesinae (Diptera, Chironomidae) from the Upper Cretaceous of the Taimyr. *Paleontol. J.*, **1976**: 78-83.

Kalugina, N.S. 1977. Paleontological data and some questions on the evolution of the Culicoidea and Chironomoidea (Diptera). IN: *Systematics and Evolution of Dipteran Insects*, pp. 25-30. Leningrad: Zoological Institute of the USSR Academy of Sciences. [In Russian.]

Kalugina, N.S. 1980. Cretaceous Aphroteniinae from north Siberia (Diptera, Chironomidae). *Electrotenia brundini* gen. nov., sp. nov. *Acta Univ. Carol., Biol.*, **12**: 89-93.

Kalugina, N.S. 1983. The Jurassic Chironomidae from Transbailkalia. IN: Narchuk, E. (Ed.), *Diptera (Insecta): Their Systematics, Geographic Distribution and Ecology*, pp. 58-60. Leningrad: USSR Academy of Sciences.

Kalugina, N.S. 1989. New psychodomorph dipteran insects from the Mesozoic of Siberia. *Paleontol. Zhur.*, **1989**(1): 65-77. [In Russian.]

Kalugina, N.S. and Kovalev, V.G. 1985. *Dipterous Insects from the Jurassic of Siberia*. Moscow: Academy of Sciences. 199 pp., 8 pls. [In Russian.]

Kaplan, V.G. 1985. On the classification and phylogeny of the Machilidae (Thysanura, Microcoryphia). *Entomol. Rev.*, 64: 117-131.

Karny, H.H. 1924. Beiträge zur Malayischen Orthopterenfauna. *Treubia*, 5: 1-234, pls. 1-2.

Karny, H.H. 1925. Cricket-locusts (Gryllacridae), chiefly from the Philippine Islands. *Phillipine J. Sci.*, 28: 131-171.

Karsch, F. 1886. Die Mekopodiden des Berliner zoologischen Museums. *Berl. Entomol. Z.*, 30: 107-118, pl. 4.

Kasimov, T. 1956. The feeding of the dragonfly larva *Anax imperator* Leach. *Izv. Akad. Nauk SSSR*, 11: 91-97.

Kathirithamby, J. 1989. Review of the Order Strepsiptera. *Syst. Entomol.*, 14: 41-92.

Kavanaugh, D.H. 1986. A systematic review of amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. *Proc. California Acad. Sci.*, 44: 67-109.

Keilbach, R. 1939. Neue Funde des Strepsipterons *Mengea tertiaria* im baltischen Bernstein. *Bernstein-forschungen*, 4: 1-7, pls. 1-2.

Keilbach, R. 1982. Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte. *Deut. Entomol. Z.*, N.F., 29: 129-286, 301-491.

Keilin, D. 1940. The early stages of the families Trichoceridae and Anisopodidae (=Rhyphidae) (Diptera: Nematocera). *Trans. Roy. Entomol. Soc.*, 90: 39-62.

Kellogg, V.L. 1893. The sclerites of the head of *Danaus archippus* Fab. *Kansas Univ. Quart.*, 2: 51-58.

Kellogg, V.L. 1895. The mouth-parts of the Lepidoptera. *Am. Nat.*, 29: 546-556.

Kellogg, V.L. 1899. The mouth parts of the nematocerous Diptera. *Psyche*, 8: 303-306, 327-330, 346-348, 363-365.

Kellogg, V.L. 1902. The development and homologies of the mouth parts of insects. *Am. Nat.*, 36: 683-706.

Kelner-Pillault, S. 1969a. Les abeilles fossiles. *Mem. Soc. Entomol. Ital.*, 48: 519-534.

Kelner-Pillault, S. 1969b. Abeilles fossiles ancetres des apides sociaux. *Proc. Sixth Congr. Int. Union Stud. Social Insects*, pp. 85-93.

Kelner-Pillault, S. 1970a. L'ambre Balte et sa faune entomologique avec description de deux apoides nouveaux. *Ann. Soc. Entomol. France*, N.S., **6**: 3-24.

Kelner-Pillault, S. 1970b. Une melpone (s. 1.) de l'ambre Balte (Hym. Apidae). *Ann. Soc. Entomol. France*, N.S., **6**: 437-441.

Kelner-Pillault, S. 1974. Stat d'evolution des apides de l'ambre Balte. *Ann. Soc. Entomol. France*, N.S., **10**: 623-634.

Kelsey, L.P. 1954. The skeleto-motor mechanism of the dobson fly, *Corydalus cornutus*. Part 1. Head and prothorax. *Cornell Univ. Agr. Exp. Stat. Mem.*, 334: 1-51.

Kelsey, L.P. 1981. Scenopinidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 525-528.

Kemp, T.S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. London: Academic Press.

Kemper, H. 1932. Beitrage zur Biologie der Bettwanze (*Cimex lectularis* L.). III. Uber den Mechanismus des Stechsaugaktes. *Z. Morphol. Okol. Tiere*, **24**: 491-518.

Kennedy, H.D. 1958. Biology and life history of a new species of mountain midge, *Deuterophlebia nielsoni*, from eastern California (Diptera: Deuterophlebiidae). *Trans. Am. Micros. Soc.*, **77**: 201-228.

Kennedy, H.D. 1960. *Deuterophlebia inyoensis*, a new species of mountain midge from the alpine zone of the Sierra Nevada Range, California (Diptera: Deuterophlebiidae). *Trans. Am. Micros. Soc.*, **79**: 191-210.

Kennedy, H.D. 1981. Deuterophlebiidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 199-202.

Kennedy, J.S. and Mittler, T.E. 1953. A method of obtaining phloem sap via the mouth-parts of aphids. *Nature*, **171**: 528.

Kernbach, K. 1967. Uber die bisher im Pliozän von Willershausen gefundenin Schmetterlings und Raupenreste. *Ber. Naturhist. Ges.*, **111**: 103-108.

Kerr, W.E. and Costa Cruz, G. 1961. Funcoẽs diferentes tomadas pela glandula mandibular na evolução das abelhas em geral e em *Trigona* (*Oxytrigona*) *tataira* em especial. *Rev. Bras. Biol.*, 21: 1-16.

Kerr, W.E. and Da Cunha, R.A. 1976. Taxonomic position of two fossil bees (Apidae). *Rev. Biol. Trop.*, 24: 35-43.

Kesavan, S.K. and Reddy, N.P. 1985. On the feeding strategy and the mechanics of blood sucking in insects. *J. Theor. Biol.*, 113: 781-783.

Kevan, D.K.M. 1982a. Orthoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 352-379. New York: McGraw-Hill Book Co.

Kevan, D.K.M. 1982b. Phasmatoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 379-383. New York: McGraw-Hill Book Co.

Kevan, D.K.M. and Cutten, F.E.A. 1981. Nymphomyiidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 203-208.

Kevan, D.K.M. and Wighton, D.C. 1981. Paleocene orthopteroids from south-central Alberta, Canada. *Can. J. Earth Sci.*, 18: 1824-1837.

Kevan, P.G. 1984. Pollination by animals and angiosperm biosystematics. IN: Grant, W.F., (Ed.), *Plant Biosystematics*, pp. 271-292. New York: Academic Press.

Kevan, P.G. and Baker, H.G. 1983. Insects as flower visitors and pollinators. *Ann. Rev. Entomol.*, 28: 407-453.

Kevan, P.G. and Baker, H.G. 1984. Insects on flowers. IN: Huffaker, C.B. and Rabb, R.L., (Eds.), *Ecological Entomology*, pp. 607-631. New York: John Wiley and Sons.

Kevan, P.G., Chaloner, W.G. and Savile, D.B. 1975. Interrelationships of early terrestrial arthropods and plants. *Palaeontology*, 18: 391-417.

Khan, M.R. 1972. The anatomy of the head-capsule and mouth-parts of *Dysdercus fasciatus* Sign. (Pyrrhocoridae, Hemiptera). *J. Nat. Hist.*, 6: 289-310.

Khatib, S.M.H. 1946. Studies in Galerucinae. The external morphology of *Galerucella birmanica* (Jacoby)--Coleoptera, Polyphaga, Phytophaga, Chrysomelidae, Galerucinae. *Proc. Indian Acad. Sci.*, (B), 23: 1-38.

Kidston, R. and Lang, W.H. 1921. On Old Red Sandstone plants showing structure from the Rhynie Chert Bed, Aberdeenshire. Part V. The Thallophyta occurring in the peat-beds; the succession of the plants throughout a vertical section of the bed, and the conditions of accumulation and preservation of the deposit. *Trans. Roy. Soc. Edinburgh*, 52: 855-902, pls. 1-10.

Kieffer, J.J. 1912. Hymenoptera. Ichneumonoidea. Evaniidae. *Das Tierreich*, 30: 1-431.

Kien, J. 1975. Motion detectors in locusts and grasshoppers. IN: Horridge, G.A., (Ed.), *The Compound Eye and Vision of Insects*, pp. 410-422. Oxford: Oxford University Press.

Killington, F.J. 1936. The imago. External morphology. IN: Killington, F.J., *A Monograph of the British Neuroptera*, pp. 13-44. London: Ray Society.

Kim, K.C. 1982. Anoplura. IN: Parker, S.K., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 406-409. New York: McGraw-Hill Book Co.

Kim, K.C. 1988. Evolutionary parallelism in Anoplura and eutherian mammals. IN: Service, M.W., (Ed.), "Biosystematics of Haematophagous Insects." *Syst. Assn. Spec. Vol.*, 37: 91-114. Oxford: Clarendon Press.

Kim, K.C. and Cook, E.F. 1966. A comparative external morphology of adult Sphaeroceridae (Diptera). *Misc. Publ. Entomol. Soc. Am.*, 5: 76-100.

Kim, K.C. and Ludwig, H.W. 1978. The family classification of the Anoplura. *Syst. Entomol.*, 3: 249-284.

Kim, K.C. and Ludwig, H.W. 1982. Parallel evolution, cladistics and classification of parasitic Psocodea. *Ann. Entomol. Soc. Am.*, 75: 537-548.

Kimmins, D.E. 1940. The genus *Stilbopteryx* Newman (Neuroptera). *Ann. Mag. Nat. Hist.*, (11), 5: 449-462.

Kimmins, F.M. and Tjallingii, W.F. 1985. Ultrastructure of sieve-element penetration by aphid stylets during electrical recording. *Entomol. Exp. Appl.*, 39: 135-141.

King, J.R. and Thompson, W.L. 1958. Fruit-piercing moth, *Gonodonta nutrix* (Cramer), attacks oranges in Florida. *Florida Entomol.*, 41: 61-65.

Kingsolver, J.G. and Daniel, T.L. 1979. On the mechanics and energetics of nectar feeding in butterflies. *J. Theor. Biol.*, **76**: 167-179.

Kinsey, A.C. 1919. Fossil Cynipidae. *Psyche*, **26**: 44-49.

Kinsey, A.C. 1937. Family Cynipidae. IN: Carpenter, F.M., et al., Insects and arachnids from Canadian amber. *Univ. Toronto Stud. Geol. Ser.*, **40**: 21-27.

Kinzelbach, R.K. 1966. Zur Kopfmorphologie der Facherflugler (Strepsiptera, Insecta). *Zool. Jb. (Anat.)*, **84**: 559-684.

Kinzelbach, R.K. 1970. Eine Gangmine aus dem eozänen Olshiefer von Messel (Insecta: ?Lepidoptera). *Paläont. Z.*, **44**: 93-96.

Kinzelbach, R.K. 1971. Morphologische Befunde an Fächerflügern und ihre phylogenetische Bedeutung. *Zoologica*, **119**: 1-256.

Kinzelbach, R.K. 1979. Das erste neotropische Fossil der Fächerflügler (Stuttgarter Bernstein-sammluing: Insecta, Strepsiptera). *Stutt. Beitr. Naturk.*, (B) **52**: 1-14.

Kinzelbach, R.K. 1983. Fächerflügler aus dem dominikanischen Bernstein (Insecta: Strepsiptera: Myrmecolacidae). *Verh. Naturwiss. Ver. Hamburg*, N.F., **26**: 29-36.

Kinzelbach, R.K. and Lutz, H. 1984. Eine neue Eintagsfliege *Misthodotes stapfi* n. sp. aus dem Rotliegenden des Nahe-Gebietes (Ephemeroptera: Permoplectoptera: Misthodotidae). *Paläont. Z.*, **58**: 247-253.

Kinzelbach, R.K. and Lutz, H. 1985. Stylopid larva from the Eocene--a spotlight on the phylogeny of the stylopids (Strepsiptera). *Ann. Entomol. Soc. Am.*, **78**: 600-603.

Kirbach, P. 1883. Uber die Mundwerkzeuge der Schmetterlinge. *Zool. Anz.*, **1883**: 553-558.

Kirbach, P. 1884. Ueber die Mundwerkzeuge der Schmetterlinge. *Arch. Naturges.*, **1**: 78-119.

Kirby, W. and Spence, W. 1815-1826. *An Introduction to Entomology, or Elements of the Natural History of Insects*, Vols. 1-4. London: Longman. 2430 pp.

Kirk, W.D.J. 1984. Pollen-feeding in thrips (Insecta: Thysanoptera). *J. Zool., London*, **204**: 107-117.

Kirk, W.D.J. 1985. Pollen-feeding and the host specificity and fecundity of flower thrips (Thysanoptera). *Ecol. Entomol.*, 10: 281-289.

Kirk, W.D.J. 1987. How much pollen can thrips destroy? *Ecol. Entomol.*, 12: 31-40.

Kirmayer, R. 1909. Bau und Entwicklung der Mundteile bei *Vespis vulgaris*. *Gegen. Morphol. Jb.*, 39: 1-30.

Klein, U. and Muller, B. 1978. Functional morphology of palp sensilla related to food recognition in *Gryllus bimaculatus* (Saltatoria, Gryllidae). *Entomol. Exp. Appl.*, 24: 291-295.

Klemm, N. 1966. Die Morphologie des Kopfes von *Rhyacophila* Pict. (Trichoptera). *Zool. Jb. (Anat.)*, 83: 1-51.

Klingauf, F.A. 1987. Feeding, adpatation and excretion. IN: Minks, A.K. and Harrewijn, P., (Eds.), *Aphids: Their Biology, Natural Enemies and Control*, A: 225-253. Amsterdam: Elsevier.

Kniepert, F.-W. 1980. Blood-feeding and nectar-feeding in adult Tabanidae (Diptera). *Oecologia*, 46: 125-129.

Knight, K.L. 1971. Comparative anatomy of the mandible of the fourth instar mosquito larva (Diptera: Culicidae). *J. Med. Entomol.*, 8: 189-205.

Knight, O.L. 1950. Fossil insect beds of Belmont, N.S.W. *Rec. Aust. Mus.*, 22: 251-253, map.

Knuth, P. 1898. *Handbuch der Blütenbiologie. I.* Leipzig: Engelmann, Publishers.

Kobayashi, Y. and Ando, H. 1988. Phylogenetic relationships among the lepidopteran and trichopteran suborders (Insecta) from the embryological standpoint. *Z. Zool. Syst. Evol.-Forsch.*, 26: 186-210.

Koch, C.L. and Berendt, G.C. 1854. Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden, und Apteren der Vorwelt (veröffenlicht und mit zusätzen versehen von A. Menge). IN: Berendt, G.C., *Die Im Bernstein Befindlichen Organischen Reste der Vorwelt*. Berlin. 124 pp.

Kolbe, H.J. 1883. Neue Beiträge zur Kenntnis der Psociden der Bernstein-Fauna. *Stett. Entomol. Z.*, 44: 186-191.

Kompantseva, T.V. 1985. Larval description and biological peculiarities of *Basanus tsushimensis* Kasz. and G. Medv. Coleoptera, Tenebrionidae) from southern Primorye Territory. *Entomol. Rev.*, 64: 35-40.

Köningsmann, E. 1976. Das phylogenetische System der Hymenoptera. Teil 1: Einführung, Grundplanmerkmale, Schwestergruppe und Fossilfunde. *Deut. Entomol. Z.*, N.F., 23: 253-279.

Köningsmann, E. 1977. Das phylogenetische System der Hymenoptera. Teil 2: "Symphyta." *Deut. Entomol. Z.*, N.F., 24: 1-40.

Köningsmann, E. 1978a. Das phylogenetische System der Hymenoptera. Teil 3: "Terebrantes" (Unterordnung Apocrita). *Deut. Entomol. Z.*, N.F., 25: 1-55.

Köningsmann, E. 1978b. Das phylogenetische System der Hymenoptera. Teil 4: Aculeata (Unterordnung Apocrita). *Deut. Entomol. Z.*, N.F., 25: 365-435.

Konow, F.W. 1897. Ueber fossile Blatt- und Halmwespen. *Entomol. Nachr.*, 23: 36-38.

Koponen, M. and Nuortera, M. 1973. Uber subfossile Wald insekten aus dem Moor Piilonsuo in Südfinland. *Acta Entomol. Fenn.*, 29: 3-84.

Korboot, K. 1964. Comparative studies of the external and internal anatomy of three species of caddis flies (Trichoptera). *Pap. Univ. Queensland Dept. Entomol.*, 2: 1-44.

Kormilev, N.A. and Popov, Y.A. 1986. The first find of a Mesozoic aradid bug fossil in North-east Siberia (Hemiptera: Aradidae). *J. Nat. Hist.*, 20: 279-282.

Korn, W. 1943. Die Muskulatur des Kopfes und des Thorax von *Myrmeleon europaeus* und ihre Metamorphose. *Zool. Jb. (Anat.)*, 68: 273-330.

Kosaroff, G. 1935. Beobachtungen über die Ernährung der Japygiden. *Mitt. Naturw. Inst. Sophia*, 8: 181-185.

Kosztarab, M. 1982. Homoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 447-470. New York: McGraw-Hill Book Co.

Koteja, J. 1974. On the phylogeny and classification of the scale insects (Homoptera, Coccinea) (discussion based on the morphology of the mouthparts). *Acta Zool. Cracov.*, 19: 267-325.

Koteja, J. 1986a. Current state of coccid paleontology. *Boll. Lab. Entomol. Agr., Naples Univ., Suppl.*, 43: 29-34.

Koteja, J. 1985. Essay on the prehistory of scale insects (Homoptera, Coccina). *Ann. Zool.*, 38: 461-503.

Koteja, J. 1986b. *Matsuococcus saxonicus* sp.n. from Saxonian amber. *Deut. Entomol. Z.*, 33: 55-63.

Koteja, J. 1988a. Eriococcid crawlers (Homoptera, Coccinea) from Baltic amber. *Pol. Pismo Entomol.*, **58**: 503-524.

Koteja, J. 1988b. *Succinikermes kulickae* gen. et sp. n. (Homoptera, Coccinea) from Baltic amber. *Pol. Pismo Entomol.* , **58**: 525-535.

Koteja, J. 1988c. *Eomatsucoccus* gen. n. (Homoptera, Coccinea) from Siberan Lower Cretaceous deposits. *Ann. Zool.*, 42: 141-163.

Kovalev, V.G. 1974. A new genus of the family Empididae (Diptera) and its phylogenetic relationships. *Palaeontol. J.*, **1974**(1): 196-204.

Kovalev, V.G. 1978. A new fly genus (Empididae) from Late Cretaceous retinites of the Taimyr. *Paleontol. J.*, **1978**(3): 351-356.

Kovalev, V.G. 1981. The oldest representatives of the Diptera with short antennae from the Jurassic in Siberia. *Paleontol. J.*, **1981**(3): 84-100.

Kovalev, V.G. 1982. Some Jurassic Diptera--rhagionids (Muscida, Rhagionidae). *Paleontol. J.*, **1982**(3): 87-99.

Kovalev, V.G. 1985. Main aspects in the evolution of Diptera Brachycera in the Mesozoic Era. IN: Skarlato, O.A., (Ed.), *Systematics of Diptera (Insecta): Ecological and Morphological Principles*, pp. 56-59. Leningrad: Zoological Institute, USSR Academy of Sciences.

Kozlov, M.A. 1968. Order Proctotrupoidea (Hymenoptera). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 237-240. Moscow: Academy of Sciences. [In Russian.]

Kozlov, M.A. 1974. Early Cretaceous ichneumon of the family Pelecinidae. *Paleontol. J.*, **1974**(1): 131-138.

Kozlov, M.A. 1975. Family Trupochalcidae. IN: Rasnitsyn, A.P., "Hymenoptera Apocrita of the Mesozoic." *Trans. Paleontol. Inst.*, **147**: 81-83.

Kozlov, M.V. 1987. New ditrysan lepidopterans from Baltic amber. *Paleontol. J.*, **1987**(4): 59-67.

Kozlov, M.V. 1988a. New moth-like Lepidoptera from the Baltic amber. *Paleontol. J.*, **1988**(4): 56-65.

Kozlov, M.V. 1988b. Paleontology of lepidopterans and problems of the phylogeny of the order Papilionida. IN: Ponomarenko, A.G., (Ed.), *The Mesozoic Biocoenotic Crisis in the Evolution of Insects*, pp. 16-69. Moscow: Academy of Sciences. [In Russian.]

Kraepelin, K. 1882. Ueber die Mundwerkzeuge der saugenden Insecten. *Zool. Anz.*, **1882**: 574-579.

Kraepelin, K. 1883. Zur Anatomie und Physiologie des Rüssels von *Musca*. *Z. Wiss. Zool.*, **39**: 683-719, pls. 40-41.

Krafchick, B. 1942. The mouthparts of blackflies with special reference to *Eusimilium lascivum* Twinn. *Ann. Entomol. Soc. Am.*, **25**: 426-434.

Krafka, J. 1923. Morphology of the head of trichopterous larvae as a basis for the revision of the family relationships. *J. New York Entomol. Soc.*, **31**: 31-52.

Kramer, J.P. 1976. Revision of the Neotropical planthoppers of the genus *Bladina* (Homoptera: Fulgoroidea: Nogodinidae). *Trans. Am. Entomol. Soc.*, **102**: 1-40.

Kramer, S. 1950. The morphology and phylogeny of auchenorhynchous Homoptera (Insecta). *Illinois Biol. Mon.*, **20**: 1-111.

Kramer, S. 1954. The musculature of the head of the phantom crane fly larva *Bittacomorpha* (Diptera, Ptychopteridae). *J. Morphol.*, **94**: 409-437.

Kramer, S. 1955. The musculature of the head of the *Corydalus* larva (Neuroptera, Sialidae). *J. Morphol.*, **96**: 1-30.

Krassilov, V.A. and Rasnitsyn, A.P. 1982. A unique find: pollen in the intestine of Early Cretaceous sawflies. *Paleontol. J.*, **1982**(4): 80-95.

Krauss, H.A. 1911. Monographie der Embien. *Zoologica*, **23**: 1-78, pls. 1-5.

Kristensen, N.P. 1968a. The anatomy of the head and the alimentary canal of adult Eriocraniidae (Lep., Dacnonympha). *Entomol. Meddel.*, **36**: 239-315.

Kristensen, N.P. 1968b. The morphological and functional evolution of the mouthparts in adult Lepidoptera. *Opusc. Entomol.*, **33**: 67-72.

Kristensen, N.P. 1968c. The skeletal anatomy of the heads of adult Mnesarcheidae and Neopseustidae (Lep., Dacnonypha). *Entomol. Meddel.*, **36**: 137-151.

Kristensen, N.P. 1975. The phylogeny of hexapod "orders." A critical review of recent accounts. *Z. Zool. Syst. Evol.-Forsch.*, 13: 1-44.

Kristensen, N.P. 1978. A new familia of Hepialoidea from South America, with remarks on the phylogeny of the Subordo Exoporia (Lepidoptera). *Entomol. Germ.*, 4: 272-294.

Kristensen, N.P. 1979. The *Mnesarchaea* proboscis, a correction (Lepidoptera: Exoporia: Mnesarchaeidae). *Entomol. Gen.*, 5: 267-268.

Kristensen, N.P. 1981. Phylogeny of insect orders. *Ann. Rev. Entomol.*, 26: 135-157.

Kristensen, N.P. 1984a. The larval head of *Agathiphaga* (Lepidoptera: Agathiphagidae) and the lepidopteran ground plan. *Syst. Entomol.*, 9: 63-81.

Kristensen, N.P. 1984b. Studies on the morphology and systematics of primitive Lepidioptera (Insecta). *Steenstrupia*, 10: 141-191.

Kristensen, N.P. and Nielsen, E.S. 1981a. Intrinsic proboscis musculature in non-ditrysian Lepidoptera-Glossata: structure and phylogenetic significance. *Entomol. Scand., Suppl.*, 15: 299-304.

Kristensen, N.P. and Nielsen, E.S. 1981b. Double-tube proboscis configuration in neopseustid moths (Lepidoptera: Neopseustidae). *Int. J. Insect Morphol. Embryol.*, 10: 483-486.

Kristensen, N.P. and Nielsen, E.S. 1983. The *Heterobathmia* life history elucidated: immature stages contradict assignment to suborder Zeugloptera (Insecta, Lepidoptera). *Z. Zool. Syst. Evol.-Forsch.*, 21: 101-124.

Krivosheina, N.P. 1979. A new member of the family Pseudopomyzidae (Diptera) in the Palearctic and the position of the family in the system of the Diptera. *Entomol. Rev.*, 58: 106-113.

Krivosheina, N.P. and Mamaev, B.M. 1967. New data on the families Hesperinidae and Pachyneuridae and their position in the order Diptera. *Zool. Zhur.*, 46: 235-247.

Krivosheina, N.P. and Mamaev, B.M. 1970. Morphology, ecology and phylogenetic relationships of the Cramptonomyiidae (Diptera, Nematocera), a family new to the fauna of the USSR. *Entomol. Rev.*, 49: 541-548.

Krogstad, B.O. 1959. Some aspects of the ecology of *Axmyia furcata* McAtee (Diptera: Sylvicolidae). *Proc. Minnesota Acad. Sci.*, 27: 175-177.

Krüger, L. 1923. Neuroptera succinica Baltica. *Stett. Entomol. Z.*, 84: 68-92.

Krystroph, H. 1961. Vergleichend-morphologische Untersuchungen an den Mundteilen bei Empididen. *Beit. Entomol.*, 11: 824-872.

Krzeminski, W. and Kovalev, V.G. 1988. The taxonomic status of *Architipula fragmentosa* (Bode) and the family Eoasilidae (Diptera) from the Lower Jurassic. *Syst. Entomol.*, 13: 55-56.

Kugler, F. 1982. Apterygota. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 328-330. New York: McGraw-Hill Book Co.

Kugler, H. 1979. Zur Bestäubung von *Echinops ritro* L. *Berl. Deut. Bot. Ges.*, 92: 637-643.

Kuhn, O. 1961. Die Tier- und Pflanzenwelt des Solnhofer Schiefers mit vollständigem Arten- und Schriftenverzeichnis. *Geol. Bavarica*, 48: 1-68.

Kühne, W.G., Kubig, L., and Schlüter, T. 1973. Eine Micropterygidae (Lepidoptera, Homoneura) aus dem mittelcretazischem Harz Westfrankreichs. *Mitt. Deut. Entomol. Ges.*, 32: 61-64.

Kühne, W.G. and Schlüter, T. 1985. A fair deal for the Devonian Arthropoda Fauna of Rhynie. *Entomol. Gen.*, 11: 91-96.

Kukalová, J. 1958. New Palaeodictyoptera (Insecta) of the Carboniferous and Permian of Czechoslovakia. *Sborn. St. Geol. Ust. Cesl. Repub.*, 25: 239-251., pl. 1.

Kukalová, J. 1963. Permian insects of Moravia. Part I. Miomoptera. *Sborn. Geol. Ved., Palaeont.*, 1: 7-52, pls. 1-16.

Kukalová, J. 1964. Permian insects of Moravia. Part II. Liomopteridea. *Sborn. Geol. Ved., Palaeont.*, 3: 39-118, pls. 1-24.

Kukalová, J. 1968. Permian mayfly nymphs. *Psyche*, 75: 310-327.

Kukalová, J. 1969. On the systematic position of the supposed Permian beetles, Tschecardocoleidae, with a description of a new collection from Moravia. *Sborn. Geol. Ved., Palaeont.*, 11: 139-160, pl. 108.

Kukalová-Peck, J. 1980. Detailed morphology of appendages (head, thorax, abdomen) in Paleozoic insects. *Abstr. 16th Int. Congr. Entomol.*, p. 21.

Kukalová-Peck, J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. *Can. J. Zool.*, 61: 1618-1669.

Kukalová-Peck, J. 1985. Ephemeroid wing venation based upon gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemerida). *Can. J. Zool.*, 63: 933-955.

Kukalová-Peck, J. 1987. New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). *Can. J. Zool.*, 65: 2327-2345.

Kukalová-Peck, J. 1988. Leg-based appendages of Carboniferous insects and their probable equivalents in Recent embryos. *Proc. 18th Int. Congr. Entomol.*, p. 72.

Kukor, J.J. and Martin, M.M. 1987. Nutritional ecology of fungus-feeding arthropods. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 791-814. New York: John Wiley and Sons.

Kulagin, N. 1905. Der Kopfbau bei *Culex* und *Anopheles*. *Z. Wiss. Zool.*, 83: 285-335.

Kumari, S. 1955. Studies on the morphology of the red cotton bug, *Dysdercus koenigii* Fabricius (Hemiptera: Pyrrhocoridae). *J. Zool. Soc. India*, 7: 127-140.

Künckel, M.J., 1875. Les Lépidoptères à trompe perforante, destructeurs des oranges (Ophidères). *C.R. Acad. Sci., Paris*, 81: 397-400.

Kuschel, G. 1959. Un curculionide del Cretaceo Superior: primer insecto fosil de Chile. *Invest. Zool. Chilenas*, 5: 49-54.

Kusnezov, N. 1941. *A Revision of Amber Lepidoptera*. Moscow and Leningrad: Academy of Sciences. 136 pp.

Kusnezov, N. 1954a. Phyletische Bedeutung der Maxillar- und Labialtaster der Ameisen. *Zool. Anz.*, 153: 28-38.

Kusnezov, N. 1954b. La formula palpal en las hormigas (Nuevos datos y algunas interpretaciones) (Hymenoptera: Formicidae). *Dusenia*, 5: 255-258.

Kvacek, Z. and Walther, H. 1974. Bemerkenswerte und seltene cinnamomoide Blätter aus dem Grenzhereich des Oligo-Miozäns Mitteleuropas. *Abh. Staatl. Mus. Min. Geol.*, 21: 197-221.

Labandeira, C.C. and Beall, B.S. 1990. Arthropod terrestriality. *Short Courses Paleontol.*, 3: in press.

Labandeira, C.C., Beall, B.S. and Hueber, F.M., 1988. Early insect diversification: evidence from a Lower Devonian bristletail from Québec. *Science*, 242: 913-916.

Labandeira, C.C., Beall, B.S. and Hueber, F.M. The oldest fossil insect and the early history of hexapods. Submitted to *Palaeontographica*, Abt. A.

LaBarbera, M. 1978. Particle capture by a Pacific brittle star: experimental test of the aerosol suspension feeding model. *Science*, 201: 1147-1149.

LaBarbera, M. 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. *Am. Zool.*, 24: 71-84.

Lacasa Ruiz, A. and Martinez Declós, Y.W. 1986. Fauna y flora de los yacimentos Neocomienses del Montsec (Prov. Lérida). *Paleontol. Evol.*, 20: 215-223.

Lacombe, D. 1964. Contribução ao estudo dos Embiidae. VII. Musculatura da região cefalica de *Embolyntha batesi* MacLachlan, 1877 (Embiidina). *Bol. Mus. Nac.(Zool.), Rio de Janeiro*, N.S., 245: 1-20.

LaGreca, M. 1939. La muscolatura di *Gryllotalpa gryllotalpa* (L.). *Arch. Zool. Ital.*, 27: 217-319.

Lall, S.B. and Davies, D.M. 1971. An intergeneric comparison of cephalic structure in tabanids (Diptera) in relation to feeding habits. *J. Med. Entomol.*, 8: 700-706.

Lambert, J.B., Frye, J.S. and Poinar, G.O., Jr. 1985. Amber from the Dominican Republic: analysis by nuclear magnetic resonance spectroscopy. *Archaeometry*, 27: 43-51.

Lambkin, K.J. 1987. A re-examination of *Euporistmites balli* Tillyard from the Palaeocene of Queensland (Neuroptera: Osmylidae: Kempyninae). *Neuropt. Int.*, 4: 295-300.

Lambkin, K.J. 1988. A re-examination of *Lithosmylidia* Riek from the Triassic of Queensland with notes on Mesozoic "osmylid-like" fossil Neuroptera (Insecta: Neuroptera). *Mem. Queensland Mus.*, 25: 445-458.

Lameere, M.A. 1917. Revision sommaire des insectes fossiles du Stephanien de Commentry. *Bull. Mus. Hist. Nat., Paris*, 23: 141-200.

Landa, V. 1969. Jepice--Ephemeroptera. *Fauna C.S.S.R.*, **18**: 1-347. Prague: Naklad. Cesk. Akad. Ved.

Langenheim, J.H. 1964. Present status of botanical studies of ambers. *Bot. Mus. Leaf., Harvard Univ.*, **20**: 225-287.

Langenheim, J.H. 1969. Amber: a botanical inquiry. *Science*, **163**: 1157-1169.

Langenheim, J.H. and Beck, C.W. 1968. Catalogue of infrared spectra of fossil resins (ambers). I. North and South America. *Bot. Mus. Leaf., Harvard Univ.*, 22: 65-120.

Langenheim, R.L., Jr., Smiley, C.J. and Gray, J. 1960. Cretaceous amber from the Arctic Coastal Plain of Alaska. *Bull. Geol. Soc. Am.*, 71: 1345-1356.

Larew, H.G. 1986. The fossil gall record: a brief summary. *Proc. Entomol. Soc. Washington*, **88**: 385-388.

Larink, O. 1970. Die Kopfbildung von *Lepisma saccharina* L. (Insecta, Thysanura). *Z. Morphol. Tiere*, **67**: 1-15.

Larink, O. 1971. Der felsenspringer *Petrobius*, Mundwerkzeuge von ursprünglichem Bau. *Mikrokosmos*, **60**: 47-49.

Larsson, S.G. 1978. Baltic amber: a palaeobiological study. *Entomonograph*, 1: 1-192.

Lass, M. 1905. Beitr"ge zur Kenntnis des histologisch-anatomischen Baues des weiblichen Hunddeflohes (*Pulex canis* Dugès s. *Pulex serraticeps* Taschenberg). *Z. Wiss. Zool.*, **79**: 73-131.

Latreille, P.A. 1832. *Cours d'Entomologie*, vol. 8. Paris.

Laurentiaux, D. 1950. Les insectes houillers du Limbourg Hollandais. *Meded Geol. Stich.*, N.S., 4: 13-22, pls. 1-5.

Laurentiaux, D. 1952. Découverte d'un homoptère prosoboloide dans le Namurien Belge. *Publ. Assn. Etude Paleont. Strat. Houl.*, **14**: 1-16, pls. 1-2.

Laurentiaux, D. 1953. Classe des insectes. IN: Piveteau, J., (Ed.), *Traité de Paleontologie*, 3: 397-527. Paris: Paul Masson.

Lauterbach, K.-E. 1972. Die morphologischen Grundlagen für die Entstehung der Entognathie bei den apterygoten Insekten in phylogenetischer Sicht. *Zool. Beitr.*, 18: 25-69.

Lavigne, R. 1979. Carabids as seed feeders (Coleoptera: Carabidae). *Cordulia*, 5: 67-69.

Lavoipierre, M.M.J. 1967. Feeding mechanism of *Haematopinus suis*, on the transilluminated mouse ear. *Exp. Parasitol.*, 20: 303-311.

Lavoipierre, M.M.J., Dickerson, G. and Gordon, R.M. 1959. Studies on the methods of feeding of blood-sucking arthropods. 1. The manner in which triatomine bugs obtain their blood meal, as observed in the tissues of the living rodent, with some remarks on the effects of the bite on human volunteers. *Ann. Trop. Med. Parasitol.*, 53: 235-250.

Lawrence, J.F. 1977a. The family Pterogeniidae, with notes on the phylogeny of the Heteromera. *Coleopt. Bull.*, 31: 25-56.

Lawrence, J.F. 1977b. Extraordinary images show how beetles have adapted to live off plants, and each other. *Horticulture*, 55: 8-13.

Lawrence, J.F. 1982. Coleoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 482-553. New York: McGraw-Hill Book Co.

Lawrence, J.F. 1987. Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invert. Taxon.*, 2: 1-53.

Lawrence, J.F. and Hlavac, T.F. 1979. Review of the Derodontidae (Coleoptera: Polyphaga) with new species from North America and Chile. *Coleopt. Bull.*, 33: 369-414.

Lawrence, J.F. and Newton, A.F., Jr. 1980. Coleoptera associated with the fruiting bodies of slime molds (Myxomycetes). *Coleopt. Bull.*, 34: 129-143.

Lawrence, J.F. and Newton, A.F., Jr. 1982. Evolution and classification of beetles. *Ann. Rev. Ecol. Syst.*, 12: 261-290.

Lawrence, J.F. and Stephan, K. 1975. The North American Cerylonidae (Coleoptera: Clavicornia). *Psyche*, 82: 131-166.

Lawrey, J.D. 1987. Nutritional ecology of lichen/moss arthropods. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 209-233. New York: John Wiley and Sons.

Lawson, J.W.H. 1951. The anatomy and morphology of the early stages of *Culicoides nubeculosus* Meigen (Diptera: Ceratopogonidae = Heleidae). *Trans. Roy. Entomol. Soc. London*, **102**: 511-570.

Lawton, J.H. 1976. The structure of the arthropod community on bracken. *Bot. J. Linn. Soc.*, **73**: 187-216.

Lawton, J.H. 1982. Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *J. Anim. Ecol.*, **51**: 573-595.

Leader, J.P. 1976. Marine caddis flies (Trichoptera: Philanisidae). IN: Cheng, L., (Ed.), *Marine Insects*, p. 291-302. New York: North Holland Publishing Company.

Leathers, A.L. 1922. Ecological study of aquatic midges and some related insects with special reference to feeding habits. *Bull. U.S. Bur. Fisheries*, **38**: 1-61.

Lee, J.-K. 1987. Development of the hair mechanosensilla on the the pupal labial palp of the butterfly, *Pieris rapae* L. (Lepidoptera: Pieridae). *Int. J. Insect Morphol. Embryol.*, **16**: 343-354.

Lee, R. 1974. Structure and function of the fasicular stylets, and the labral and cibarial sense organs of male and female *Aedes aegypti* (L.) (Diptera, Culicidae). *Quaest. Entomol.*, **10**: 187-215.

Leech, H.B. and Chandler, H.P. 1956. Aquatic Coleoptera. IN: Usinger, R.L., (Ed.), *Aquatic Insects of California, with Keys to North American Genera and California Species*, pp. 293-371. Berkeley: University of California Press.

Leeson, H.S. 1939. Longevity of *Anopheles maculipennis* race *atroparvus* Van Thiel, at controlled temperature and humidity after a blood meal. *Bull. Entomol. Res.*, **30**: 295-301.

Lengerken, H. 1938. Beziehungen zwischen der Ernahrungweise und der Gestaltung der Mandibeln bei den Larven der Silphini (Coleopt.). *Zool. Anz.*, **122**: 171-175.

Léon, N. 1892. Labialtaster bei den Hemipteren. *Zool. Anz.*, **1892**: 145-147.

Léon, N. 1894. Schmidt's Lippentaster. *Zool. Anz.*, **17**: 389-399.

Léon, N. 1897. Beiträge zur Kenntnis des Labiums der Hydrocoren. *Zool. Anz.*, **1897**: 73-77.

Levasseur, L. 1965. Revision des genres voisins de *Pachorhopala* (1re partie) (Col. Staphylinidae, Zyrasini). *Ann. Soc. Entomol. France*, N.S., 1: 567-607.

Levereault, P. 1936. The morphology of the Carolina mantis. *Univ. Kansas Sci. Bull.*, 24: 205-221.

Levin, D.A. 1973. The role of trichomes in plant defense. *Quart. Rev. Biol.*, 48: 3-15.

Lew, T.-W. 1933. Head characteristics of the Odonata, with special reference to the development of the compound eye. *Entomol. Am.*, 14: 41-97.

Lewis, D.J. 1975. Functional morphology of the mouth parts in New World phlebotomine sandflies (Diptera: Psychodidae). *Trans. Roy. Entomol. Soc. London*, 124: 497-532.

Lewis, S.E. 1969. Lepidopterous larval-mining of an oak(?) leaf from the Latah Formation (Miocene) of eastern Washington. *Ann. Entomol. Soc. Am.*, 62: 1210-1211.

Lewis, S.E. 1970. Fossil caddisfly cases (Trichoptera) from the Cobb's Creek site (Cretaceous) near New Ulm, Minnesota. *Ann. Entomol. Soc. Am.*, 63: 1779-1780.

Lewis, S.E. 1971a. A new species of fossil Diptera (Diopsidae) from the Ruby River Basin (Oligocene) of Montana. *Ann. Entomol. Soc. Am.*, 64: 959-960.

Lewis, S.E. 1971b. Three new species of fossil Diptera (Bibionidae) from the Ruby River Basin (Oligocene) of southwestern Montana. *Ann. Entomol. Soc. Am.*, 64: 1464-1466.

Lewis, T. 1973. *Thrips, Their Biology, Ecology and Economic Importance*. London: Academic Press. 349 pp.

Liebermann, J. 1968. Las mandibulas en tucuras de la subfamilia Chilacridinae (Orth. Acrididae). *Rev. Invest. Agropec. Patol. Veg.*, (5), 5: 53-62.

Lillegraven, J.A. 1974. Biological considerations of the marsupial-placental dichotomy. *Evolution*, 29: 707-722.

Lin, Qi-bin. 1976. The Jurassic insects from western Liaoning. *Acta Paleontol. Sinica*, 15: 97-116, pls. 1-3.

Lin, Qi-bin. 1980. *Zhe-Wan Zhongshengdai Huoshan Chenji Van Diceng De Huafen Ji Duibi*, pp. 211-234. Beijing: Zhongguo Kexueyuan. [In Chinese.]

Lindner, E. 1938. Rhagionidae. *Die Fliegen der Palaearktischen Region*. Band IV, 20. Stuttgart: E. Schweizerb. Verlagsbuch.

Lindner, H. 1919. Uber die Mundwerkzeuge einiger Dipteren und ihre Beziehungen zur Ernahrungsweise. *Zool. Anz.*, 50: 19-27.

Lindroth, C.H. 1973. Systematics specializes between Fabricius and Darwin: 1800-1859. IN: Smith, R.F., Mittler, T.E. and Smith, C.N., (Eds.), *History of Entomology*, pp. 119-154. Palo Alto, CA: Annual Reviews, Inc.

Linsley, E.G. and MacSwain, J.W. 1950. New western species of Rhipiphoridae (Coleoptera). *Wasmann J. Biol.*, 8: 229-239.

Littig, K.S. 1942. External anatomy of the Florida walking stick, *Anisomorpha buprestoides* Stoll. *Florida Entomol.*, 25: 33-41.

Little, C. 1983. *The Colonisation of Land: Origins and Adaptations of Terrestrial Animals*. Cambridge: Cambridge University Press. 290 pp.

Liu, C.L. 1925. Observations on the acroglossal buttons and on the submentum of Hymenoptera. *Ann. Entomol. Soc Am.*, 28: 445-454.

Livingstone, D. 1969. On the morphology and biology of *Tingis buddleiae* Drake (Heteroptera: Tingidae). Part II. The functional anatomy of the head. *J. Anim. Morphol. Physiol.*, 16: 135-189.

Lloyd, J.U. and Lloyd, C.G. 1921. The biology of North American caddis fly larvae. *Bull. Lloyd Libr., Entomol. Ser.*, 21: 1-124.

Lo, S.E. and Acton, A.B. 1969. The ultrastructure of the rostral sensory organs of the water bugs *Ctenocorixa bifida* (Hungerford) (Hemiptera). *Can. J. Zool.*, 47: 717-722.

Lobanov, A.M. 1970. [The] morphology of last instar larvae of Helomyzidae (Diptera). *Zool. Zhur.*, 49: 1671-1675. [In Russian.]

Loew, H. 1850. *Uber den Bernstein und die Bernsteinfauna*. Programm Realschule Meseritz, pp. 1-44.

Loew, H. 1851. Beschriebung einiger neuer *Tipularia terricola*. *Linn. Entomol.*, 1851: 385-406.

Loew, H. 1861. Uber die Dipterenfauna des Bernsteins. *Amtl. Ber. Vers. Deut. Naturforsch.*, 35: 88-98.

Lombardi, D. 1928. Contributo alla conoscenza dello *Scirtes hemisphaericus* L. (Coleoptera-Helodidae). *Boll. Ist. Entomol., Univ. Bologna*, 1: 236-258.

Lopez, A.W. 1932. Morphological studies of the head and mouthparts of the mature codling-moth larva *Carpocapsa pomonella* (Linn.). *Univ. California Publ. Entomol.*, 5: 19-36.

Lorenz, H. and Kraus, M. 1957. Die Larvalsystematik der Blattwespen (Tenthredinoidea und Megalodontoidea). *Abh. Larval-syst. Ins.*, 1: 1-339.

Lorenz, R.E. 1961. Biologie und Morphologie von *Micropteryx calthella* (L.). *Deut. Entomol. Z.*, N.F., 8: 1-23.

Louveaux, A. 1972. Equipment sensoriel et système nerveaux périphérique des pièces buccales de *Locusta migratoria* L. *Ins. Soc.*, 19: 359-368.

Louveaux, A. 1975. Etude de l'innervation sensorielle de l'hypopharynx de larves de *Locusta migratoria migratoides* R. et F. (Orthoptère, Acrididae). *Ins. Soc.*, 22: 3-12.

Louveaux, A. 1978. Feeding mechanisms of the migratory locust, *Locusta migratoria migratoroides* (Orthoptera, Acrididae). *Entomol. Exp. Appl.*, 24: 318-319.

Lowe, E.J. 1898. *Fern Growing*. New York: Trustlove and Comba.

Lozinski, P. 1908. Beitrag zur Anatomie und Histologie der Mundwerkzeuge der Myrmeleonidenlarven. *Zool. Anz.*, 33: 473-484.

Lubin, Y.D. 1983. Nasutitermes (comejen, horminga blanca, nasute termite, arboreal termite). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 743-745. Chicago: University of Chicago Press.

Luca, Y. de. 1965. Remarques morphologiques et chetotaxiques sur *Bruchidus albosparsus* (Col. Bruchidae). *Ann. Soc. Entomol. France*, N.S., 1: 479-487.

Lucas, R. 1893. Kenntnis der Mundwerkzeuge der Trichoptera. *Arch. Naturges.*, 59: 285-330.

Lucas, W.J. 1924. Labium (second maxillae) of the Paraneuroptera (Odonata). *Proc. So. London Entomol. Nat. Hist. Soc.*, 1924: 57-63, pls. 7-8.

Lucas, W.J. 1930. *The Aquatic (Naiad) Stage of the British Dragonflies (Paraneuroptera)*. London: Dulau and Co. 132 pp., 35 pls.

Ludwig, C.E. 1949. Embryology and morphology of the larval head of *Calliphora erythrocephala* (Meigen). *Microentomology*, 14: 75-111.

Lutz, H. 1985a. Eine fossile Stielaugenfliege aus dem Unter-Oligozän von Cereste, Frankreich (Diptera, Diopsidae). *Paläont. Z.*, **59**: 75-78.

Lutz, H. 1985b. Eine fossile Stechmücke aus dem Unter-Oligocän von Cereste, Frankreich (Diptera: Culicidae). *Paläont. Z.*, **59**: 269-275.

Lutz, H. 1987. Die Insekten-Thanatocoenose aus dem Mittel-Eozän der "Grube Messel" bei Darmstadt: Erste Ergebnisse. *Cour. Forsch.-Inst. Senck.*, **91**: 189-201.

Maa, T.C. 1966. Studies in Hippoboscidae (Diptera). Part 2. *Pac. Ins. Mon.*, **10**: 1-148.

Maa, T.C. and Peterson, B.V. 1987. Hippoboscidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, **28**: 1271-1281.

MacGill, E.I. 1947. The anatomy of the head and mouth-parts of *Dysdercus intermedius* Dist. *Proc. Zool. Soc. London*, **117**: 115-128.

MacKay, M.F. 1969. Microlepidopterous larvae in Baltic amber. *Can. Entomol.*, **101**: 1173-1180.

MacKay, M.R. 1970. Lepidoptera in Cretaceous amber. *Science*, **167**: 379-380.

MacKay, M.R. 1972. Larval sketches of some Microlepidoptera, chiefly North American. *Mem. Entomol. Soc. Canada*, **88**: 1-83.

MacLeay, W.S. 1821. *Horae Entomologicae, or Essays on the Annulose Animals*. London: 524 pp.

MacLeod, E.G. 1970. The Neuroptera of the Baltic amber. I. Ascalaphidae, Nymphidae, and Psychopsidae. *Psyche*, **77**: 147-180.

Macloskie, G. 1884. Kraepelin's proboscis of *Musca*. *Am. Nat.*, **18**: 1234-1244.

Madden, A.H. 1944. The external morphology of the adult tobacco hornworm (Lepidoptera, Sphingidae). *Ann. Entomol. Soc. Am.*, **37**: 145-160.

Maillet, P. 1957. Contribution a l'etude de la biologie du *Phylloxera* de la vigne. *Ann. Sci. Nat., Zool.*, Zool., (11), **19**: 283-410.

Maiz, D. and Hintze-Podufal, C. 1979. Bau und Verteilung von Sinnesorganen auf dem Clypeolabrum, Hypopharynx und der Mandibel der Schabe *Gromphadorhina brunneri*, Butler (Blaberoidea, Oxyhaloidae). *Zool. Jb. (Anat.)*, 102: 249-266.

Makel, M. 1942. Metamorphose und Morphologie des *Pseudococcus* Mannchens mit besonderer Berucksichtigung des Skelettmuskel-systems. *Zool. Jb. (Anat.)*, 67: 461-512.

Makhan'ko, Y.V. 1973. The degree of parasitism and the structure of oral teeth in synanthropic flies of the genera *Hydrotaea* R.-D. and *Musca* L. (Diptera, Muscidae). *Entomol. Rev.*, 52: 485-494.

Maki, T. 1936. Studies of the skeletal structure musculature and nervous system of the alder fly *Chauliodes formosanus* Petersen. *Mem. Fac. Sci. Agr. Taihoku Imp. Univ.*, 16: 117-243.

Malloch, J.R. 1917. A preliminary classification of Diptera, exclusive of Pupipara, based upon larval and pupal characters, with keys to imagines in certain families. Part 1. *Illinois State Lab. Nat. Hist.*, 12: 161-410, pls. 28-57.

Malyshev, S.I. 1968. *Genesis of the Hymenoptera and the Phases of Their Evolution*. London: Methuen and Co., Ltd. 319 pp.

Mamaev, B.M. and Krivosheina, N.P. 1966. New data on the taxonomy and biology of the family Axmyiidae (Diptera). *Entomol. Rev.*, 45: 93-99.

Mamaev, B.M. and Krivosheina, N.P. 1969. New data on the morphology and ecology of the Hyperoscelidae (Diptera, Nematocera). *Entomol. Rev.*, 48: 594-599.

Mamet, R. 1954. A monograph of the Conchaspididae Green (Hemiptera: Coccoidea). *Trans. Roy. Entomol. Soc. London*, 105: 189-239.

Mangan, J. 1909. On the mouth-parts of some Blattidae. *Proc. Roy. Irish Acad.*, (B), 27: 1-10.

Manning, D.L. 1978. Mouthparts of larva of *Opifex fuscus* and *Aedes australis* (Diptera: Culicidae); a scanning electron microscope study. *New Zealand J. Zool.*, 5: 801-806.

Manton, S.M. 1960. Concerning head development in the arthropods. *Biol. Rev.*, 35: 265-282.

Manton, S.M. 1964. Mandibular mechanisms and the evolution of arthropods. *Philos. Trans. Roy. Soc. London*, (B), 247: 1-183.

Manton, S.M. 1977. *The Arthropoda: Habits, Functional Morphology and Evolution*. Oxford: Oxford Univ. Press. 527 p.

Manton, S.M. 1979. Functional morphology and the evolution of the hexapod classes. IN: Gupta, A.P., (Ed.), *Arthropod Phylogeny*, pp. 387-465. New York: Van Nostrand Reinhold Co.

Marchal, P. 1906. Recherches sur la biologie et le developpement des Hymenopteres parasites: Les platygasters. *Arch. Zool. Exp. Gen.*, (4), 4: 485-640, pls. 17-24.

Mari Mutt, J. 1983. Collembola in amber from the Dominican Republic. *Proc. Entomol. Soc. Washington*, **85**: 575-587.

Marks, E.P. 1957. The food pump of *Pelocoris* and comparative studies on other aquatic Hemiptera. *Psyche*, **64**: 123-134.

Marlatt, C.L. 1895a. The hemipterous mouth. *Proc. Entomol. Soc. Washington*, **3**: 241-249.

Marlatt, C.L. 1895b. The currant stem-girdler. *Insect Life*, **7**: 387-390.

Marquardt, F. 1939. Beitrage zur Anatomie der Muskulatur und der peripheren Nerven von *Carausius* (*Dixippus*) *morosus* Br. *Zool. Jb. (Anat.)*, **66**: 63-128.

Marshall, A.G. 1987. Nutritional ecology of ectoparasitic insects. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 721-739. New York: John Wiley and Sons.

Marshall, W.S. 1914. On the anatomy of the dragonfly *Libellula quadrimaculata*. *Trans. Wisconsin Acad. Sci.*, **17**: 755-790.

Martin, B. 1986. Hymenoptera and pollination. IN: Betts, C., Laffoley, D.A. and Cribb, P.W., (Eds.), *The Hymenopterist's Handbook*, pp. 83-90. Hanworth, Great Britain: The Amateur Entomologist's Society.

Martinez-Delclós, X. 1989. *Chresmoda aquatica* n.sp. Insecto Chresmodidae del Cretacico Inferior de la Sierra del Montsec (Lleida, España). *Rev. Espanola Palaeontol.*, **4**: 67-74.

Martynov, A.V. 1925. To the knowledge of fossil insects from Jurassic beds in Turkestan. Part 2. *Izd. Acad. Sci. USSR*, **19**: 569-598. [In Russian.]

Martynov, A.V. 1926. To the knowledge of fossil insects from Jurassic beds in Turkestan. 5. On some interesting Coleoptera. *Ezheg. Russ. Paleontol. Obshch.*, 5: 1-38. [In Russian.]

Martynov, A.V. 1927a. *Jurassic Fossil Mecoptera and Paratrichoptera from Turkestan and Ust-Balei (Siberia)*. Moscow: Academy of Sciences. [In Russian.]

Martynov, A.V. 1927b. Jurassic fossil insects from Turkestan. 7. Some Odonata, Neuroptera, Thysanoptera. *Izv. Acad. Sci. USSR*, 1927: 757-768. [In Russian.]

Martynov, A.V. 1928. A new fossil form of Phasmatodea from Galkino (Turkestan) and on Mesozoic phasmids in general. *Ann. Mag. Nat. Hist.*, (10), 1: 319-328.

Martynov, A.V. 1930. Paleozoic insects from the Kuznetsk Basin. *Izv. Glav. Geol. Razved. Uprov.*, 49: 73-100. [In Russian.]

Martynov, A.V. 1932. New Permian Palaeoptera with a discussion of some problems of their evolution. *Trans. Paleontol. Inst.*, 1: 1-44.

Martynov, A.V. 1937a. Liassic insects from Shurab and Kisyl-Kiya. *Trans. Paleontol. Inst.*, 7(1): 1-232.

Martynov, A.V. 1937b. Permian fossil insects from Kargala and their relationships. *Trans. Paleontol. Inst.*, 7(2): 1-92.

Martynov, A.V. 1938a. Review of localities of fossil insects in the USSR. *Trans. Paleontol. Inst.*, 7(3): 6-28.

Martynov, A.V. 1938b. Studies on the geological history and phylogeny of the orders of insects (Pterygota). *Trans. Paleontol. Inst.*, 7(4): 1-149. [In Russian.]

Martynov, A.V. 1940. Permian fossil insects from Chekarda. *Trans. Paleontol. Inst.*, 11(1): 1-62, pls. 1-6. [In Russian.]

Martynova, O.M. 1958. New insects from Permian and Mesozoic deposits of the USSR. *Mat. Prob. Paleontol.*, 2: 69-94.

Martynova, O.M. 1959. Phylogenetic interrelationships of the mecopteroid insect complex. *Trans. Severtzov Inst. Anim. Morphol.*, 27: 221-230. [In Russian.]

Martynova, O.M. 1961. Superorders Neuropteroidea, Mecopteroidea. IN: Rohdendorf, B.B., Bekker-Migdisova, E.E., Martynova, O.M and Sharov, A.G., "Paleozoic Insects from the Kusnetsk Basin." *Trans. Paleontol. Inst.*, 85: 469-593.

Martynova, O.M. 1962. Order Neuroptera. IN: Rohdendorf, B.B., (Ed.), *Osnovy Paleontologii*, pp. 272-282. Moscow: Academy of Sciences. [In Russian.]

Masner, L. 1969. A scelionid wasp surviving unchanged since Tertiary (Hymenoptera: Proctotrupoidea). *Proc. Entomol. Soc. Washington*, 71: 397-400.

Masner, L. 1976. Revisionary notes and keys to World genera of Scelionidae (Hymenoptera: Proctotrupoidea). *Mem. Entomol. Soc. Canada*, 97: 1-87.

Masner, L. and Dessart, P. 1967. La reclassification des catégories taxonomiques superieures des Ceraphronoidea (Hymenoptera). *Bull. Inst. Roy. Sci. Nat. Belgique*, 43: 1-33.

Mason, W.R.M. 1978. A new genus, species, and family of Hymenoptera (Ichneumonoidea) from Chile. *Proc. Entomol. Soc. Washington*, 80: 606-610.

Mathur, A.C. 1956. Studies on *Brachythemis contaminata* Fabricus Libellulidae, Odonata). Part I. Head and its musculature. *Indian J. Entomol.*, 18: 372-388.

Mathur, K.C. 1962. The musculature of the head capsule and mouth parts of adult *Pantala flavescens* (Fabricus) (Odonata, Anisoptera, Libellulidae, Libellulinae). *J. Anim. Morphol. Physiol.*, 9: 18-31.

Mathur, P.N. and Mathur, K.C. 1961a. Morphology of the head capsule and its appendages of *Orthetrum taeniolatum* Schneider (Odonata, Anisoptera, Libellulidae, Libellulinae). *Proc. Indian Acad. Sci.*, (B), 53: 187-203.

Mathur, P.N. and Mathur, K.C. 1961b. Studies on the cephalic musculature of adult *Ictinus angulosus* Selys (Odonata, Anisoptera, Gomphidae, Ictinae). *J. Morphol.*, 109: 237-249.

Matile, L. 1981. Description d'un Keroplatidae du Cretace Moyen et données morphologiques et taxonomiques sur les Mycetophiloidea (Diptera). *Ann. Soc. Entomol. France*, N.S., 17: 99-123.

Matsuda, R. 1956. Musculature of the head of *Aguilla adnixa* (Hagen) (Neuroptera, Raphidiidae). *J. Kansas Entomol. Soc.*, 29: 146-155.

Matsuda, R. 1957. Morphology of the head of a sawfly, *Macrophya pluricincta* Norton (Hymenoptera, Tenthredinidae). *J. Kansas Entomol. Soc.*, 30: 99-109.

Matsuda, R. 1965. Morphology and evolution of the insect head. *Mem. Am. Entomol. Inst.*, 4: 1-334.

Matthews, E.G. 1972. A revision of the Scarabaeinae dung beetles of Australia. *Aust. J. Zool., Suppl.*, **9**: 1-330.

Matthews. E.G. 1976. *Insect Ecology*. St. Lucia, Queensland: Univ. Queensland Press. 226 p.

Mattingly, P.F. 1965. The evolution of parasite-arthropod vector systems. IN: Taylor, A.E.R., (Ed.), *The Evolution of Parasite-Arthropod Vector Systems*, pp. 29-45. Oxford: Blackwell Publications.

Mattingly, R.L. 1987a. Resource utilization by the freshwater deposit feeder *Ptychoptera townesi* (Diptera: Ptychopteridae). *Freshw. Biol.*, **18**: 241-253.

Mattingly, R.L. 1987b. Handling of coarse and fine particulate organic matter by the aquatic insects *Paraleptophlebia gregalis* and *P. temporalis* (Ephemeroptera: Leptophlebiidae). *Freshw. Biol.*, **18**: 255-265.

Mattson, W.J. and Scriber, J.M. 1987. Nutritioinal ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 105-146. New York: John Wiley and Sons.

Mayer, K. 1955. Der Parasitismus der Heleiden (Ceratopogoniden) Dipt. *Z. Angew. Zool.*, 42: 95-107.

Mazokhin-Porshnyakov, G.A. 1975. Investigations on the vision of ants. IN: Horridge, G.A., (Ed.), *The Compound Eye and Vision of Insects*, pp. 114-120. Oxford: Oxford University Press.

McAllan, J.W. and Adams, J.B. 1961. The significance of pectinase in plant penetration by aphids. *Can. J. Zool.*, **39**: 305-310.

McAlpine, D.K. 1966. Description and biology of an Australian species of Cypselosomatidae (Diptera), with a discussion of family relationships. *Aust. J. Zool.*, **14**: 673-685.

McAlpine, D.K. 1978. Description and biology of a new genus of flies related to *Anthoclusia* and representing of a new family (Diptera, Schizophora, Neurochaetidae). *Ann. Natal. Mus.*, **23**: 273-295.

McAlpine, J.F. 1967. A detailed study of Ironomyiidae (Diptera: Phoroidea). *Can. Entomol.*, **99**: 225-236.

McAlpine, J.F. 1970. First record of calypterate flies in the Mesozoic Era (Diptera: Calliphoridae). *Can. Entomol.*, **102**: 342-346.

McAlpine, J.F. 1973. A fossil ironomyiid fly from Canadian amber (Diptera: Ironomyiidae). *Can. Entomol.*, **105**: 105-111.

McAlpine, J.F. 1981. Morphology and terminology--adults. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 9-63.

McAlpine, J.F. 1989. Phylogeny and classification of the Muscomorpha. IN: McAlpine, J.F. and Wood, D.M., (Eds.), "Manual of Nearctic Diptera," vol. 3. *Res. Branch Agr. Canada*, **32**: 1397-1518.

McAlpine, J.F., et al., (Eds.). 1981. Manual of Nearctic Diptera. Vol. 1. *Res. Branch Agr. Canada*, **27**: 1-674.

McAlpine, J.F., et al., (Eds.). 1987. Manual of Nearctic Diptera. Vol. 2. *Res. Branch Agr. Canada*, **28**: 675-1332.

McAlpine, J.F. and Wood, D.M., (Eds.). 1989. Manual of Nearctic Diptera. Vol. 3. *Res. Branch Agr. Canada*, **32**: 1333-1518.

McAlpine, J.F. 1987a. Periscelididae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera." Vol. 2. *Res. Branch Agr. Canada*, **28**: 895-898.

McAlpine, J.F. 1987b. Curtonotidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera." Vol. 2. *Res. Branch Agr. Canada*, **28**: 1007-1010.

McAlpine, J.F. 1987c. Diastatidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera." Vol. 2. *Res. Branch Agr. Canada*, **28**: 1019-1022.

McAlpine, J.F. 1989. Phylogeny and classification of the Muscomorpha. IN: McAlpine, J.F. and Wood, D.E., (Eds.), "Manual of Nearctic Diptera," vol. 3. *Res. Branch Agr. Canada*, **32**: 1397-1518.

McAlpine, J.F. and Martin, J.E.H. 1966. Systematics of Sciadoceridae and relatives with descriptions of two new genera and species from Canadian amber and erection of Family Ironomyiidae (Diptera: Phoroidea). *Can. Entomol.*, **98**: 527-544.

McAlpine, J.F. and Martin, J.E.H. 1969. Canadian amber--a paleontological treasure-chest. *Can. Entomol.*, **101**: 819-838.

McAtee, W.L. and Malloch, J.R. 1928. Synopsis of pentatomid bugs of the subfamilies Megaridinae and Canopinae. *Proc. U.S. Natl. Mus.*, **72**: 1-21.

McCafferty, W.P. and Provonsha, A.V. 1981. *Aquatic Entomology: The Fishermen's and Ecologists' Illustrated Guide to Insects and Their Relatives*. Boston: Jones & Bartlett Publ., Inc. 448 p.

McClenahan, E.M. 1904. The development of the rostrum in rhynchophorous Coleoptera. *Psyche*, 11: 89-101, pls. 6-9.

McClure, M.S. 1983. Myrmeleon (horminga leon, ant lion). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 742-743. Chicago: University of Chicago Press.

McIver, S.B. and Sutfliffe, J.F. 1986. Sensory basis of behavior and structural adaptations for feeding in black flies. IN: Kim, K.C. and Merritt, R.W., (Eds.), *Black Flies: Ecology, Population Management, and Annotated World List*, pp. 228-249. University Park, PA: Pennsylvania State University Press.

McKay, I.J. and Rayner, R.J. 1986. Cretaceous fossil insects from Orapa, Botswana. *J. Entomol. Soc. So. Africa*, 49: 7-17.

McKeever, S. 1986. Mouthparts of the four North American *Corethrella* species (Diptera: Chaoboridae), with detailed study of *C. appendiculata*. *J. Med. Entomol.*, 23: 502-512.

McKeever, S., Wright, M.D. and Hagan, D.V. 1988. Mouthparts of females of four *Culicoides* species (Diptera: Ceratopogonidae). *Ann. Entomol. Soc. Am.*, 81: 332-341.

McKenzie, H.L. 1967. *Mealybugs of California*. Berkeley: University of California Press.

McLellan, I.D. 1968. A revision of the genus *Notonemoura* (Plecoptera: Notonemouridae). *Trans. Roy. Soc. New Zealand, Zool.*, 10: 133-140.

McNamara, C. 1924. The food of Collembola. *Can. Entomol.*, 56: 99-105.

Medvedev, G.S. 1960. The muscles of the mouth parts and pharyngeal region in Tenebrionidae (Coleoptera) of Turkmenia. *Entomol. Rev.*, 39: 69-79.

Medvedev, L.N. 1968. Leaf-cutting beetles from the Jurassic of Karatau Coleoptera, Chrysomelidae). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 155-165. Moscow: Academy of Sciences.

Medvedev, L.N. 1969. New Mesozoic Coleoptera (Cucujoidea) of Asia. *Paleontol. J.*, 1969(1): 108-113.

Medvedev, S.I. and Vysotskaya, S.O. 1969. Coleoptera from the nests of small mammals of the Transcarpathian region. *Entomol. Obozr.*, 48: 787-800.

Meek, W.J. 1903. On the mouth-parts of the Hemiptera. *Univ. Kansas Sci. Bull.*, 2: 257-277.

Meijere, J.C.H. 1916. Zur Kenntnis des Kopfbaues der Dipteren-larven und -imagines. *Zool. Anz.*, 46: 241-251.

Meikle, A.A. 1937. The insects associated with bracken. *Agr. Prog.*, 14: 58-60.

Meinander, M. 1975. Fossil Conipterygidae (Neuroptera). *Not. Entomol.*, 55: 53-57.

Meinert, F. 1880. Sur la conformation de la tête et sur l'interpretation des organes buccaux chez les insectes, ainsi que sur la systematique de cet ordre. *Entomol. Tidsk.*, 1: 147-153.

Meinert, F. 1882. Die Muntheile der Dipteren. *Zool. Anz.*, 1882: 570-574.

Meinert, F. 1886. De eucephale mygglarver. *Kong. Danske Viden. Selsk. Skrif. Sjette Raek.*, 6: 373-393.

Meinert, F. 1887. Die Unterlippe der Käfer-Gattung *Stenus*. *Zool. Anz.*, 1887: 136-139.

Meinert, F. 1888. *Scydmaenus*-larven. *Entomol. Meddel.*, 1: 144-150.

Melander, A.L. 1949. A report on some Miocene Diptera from Florissant, Colorado. *Am. Mus. Novit.*, 1407: 1-63.

Mendes, L.F. 1988. Sur deux nouvelles Nicoletiidae (Zygentoma) cavernicoles de Grèce et de Turquie et remarques sur la systématique de la famille. *Rev. Suisse Zool.*, 95: 751-772.

Menees, J.H. 1958a. The maxilla and labium of the larva of *Anopheles quadrimaculatus* Say. *Bull. Brooklyn Entomol. Soc.*, 53: 25-38.

Menees, J.H. 1958b. The facial areas, labrum, epipharynx, hypopharynx and mandibles of the larva of *Anopheles quadrimaculatus* Say. *Bull. Brooklyn Entomol. Soc.*, 53: 124-140.

Menees, J.H. 1962. The skeletal elements of the gnathocephalon and its appendages in the larvae of higher Diptera. *Ann. Entomol. Soc. Am.*, 55: 607-616.

Menge, A. 1856. *Lebenszeichen Vorwelticher im Bernstein Eingeschlossener Thiere. Program der Offenlichen Präfung der schüller der Petrischule.* Danzig. 32 pp.

Menge, A. 1866. Uber ein Rhipidopteron und einge andere im Bernstein eingeschlossene Tiere. *Schrift. Nat. Ges. Danzig*, N.F., 1: 2-5.

Menzel, R. 1975. Colour receptors in insects. IN: Horridge, G.A., (Ed.), *The Compound Eye and Vision of Insects*, pp. 121-153. Oxford: Oxford University Press.

Merritt, R.W. and Craig, D.A. 1987. Larval mosquito (Diptera: Culicidae) feeding mechanisms: mucosubstance production for capture of fine particles. *J. Med. Entomol.*, 24: 275-278.

Merritt, R.W. and Cummins, K.W., (Eds.) 1984. *An Introduction to the Aquatic Insects of North America*, 2nd edn. Dubuque, Iowa: Kendall/Hunt Publishing Company. 722 pp.

Merritt, R.W. and Schlinger, E.I. 1984. Aquatic Diptera, part two. Adults of aquatic Diptera. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 467-490. Dubuque, IA: Kendall/Hunt Publ. Co.

Merritt, R.W. and Wallace, J.B. 1981. Filter-feeding insects. *Sci. Am.*, 244: 132-144.

Messner, B. 1988. Sind die Insektenpirare oder secundare Wasserbewohner? *Deut. Entomol. Z.*, 35: 355-360.

Metcalf, C.L. 1929. The mouthparts of insects. *Trans. Illinois St. Acad. Sci.*, 21: 109-135.

Metcalf, C.L. and Flint, W.P. 1932. *Fundamentals of Insect Life*, 1st edn. New York: McGraw-Hill Book Co. 581 p.

Metcalf, C.L., Flint, W.P. and Metcalf, R.L. 1962. *Destructive and Useful Insects: Their Habits and Control*, 4th edn. New York: McGraw-Hill Book Co.

Meunier, F. 1898. Revue critique de quelques insectes fossiles du musée paleontologique de Munich. *Arch. Mus. Teyler*, (2), 6: 85-149, pls. 1-30.

Meunier, F. 1899a. Etude de quelques diptéres de l'ambre Tertiare. *Bull. Soc. Entomol. France*, 1899: 334-335, 358-359, 392-393.

Meunier, F. 1899b. Revision des diptères fossiles, types de Loew conservées au Muksee Provencial de Koenigsberg. *Misc. Entomol.*, 1899: 161-165, 169-182.

Meunier, F. 1903. Nuevas contribuciones á la fauna de los himeró-pteros fósiles. *Mem. Real Acad. Cien. Artes Barcelona*, 4(34): 1-12.

Meunier, F. 1904a. Sur une Cicadine du Kiméridgien de la Sierra del Montsech (Catalogne). *Feuille Jeun. Nat.*, 34: 119-121.

Meunier, F. 1904b. Eine neue Blattinaria aus der oberen Steinkohlenformation. *Jb. Preuss. Geol. Landsanst.*, 24

Meunier, F. 1904c. Monographie des Cecidomyidae, des Sciaridae, des Mycetophilidae et des Chironomidae de l'ambre. *Ann. Soc. Sci. Bruxelles*, 28: 12-275.

Meunier, F. 1904d. Scatopsidae im baltischen Bernstein. *Jb. Geol. Landesanst.*, 24: 392-395.

Meunier, F. 1905a. Sur deux Mymaridae de l'ambre de la Baltique. *Misc. Entomol.*, 12: 1-4.

Meunier, F. 1905b. Contribution à la faune des Acalyptères Agromyzinae de l'ambre. *Ann. Soc. Sci. Bruxelles*, 29: 89-94, pl. 29.

Meunier, F. 1906a. Les Tipulidae de l'ambre de la Baltique. *Ann. Soc. Sci. Bruxelles*, 30: 213-215.

Meunier, F. 1906b. Monographie des Tipulidae et des Dixidae de l'ambre de la Baltique. *Ann. Soc. Nat. Zool.*, 4: 349-401.

Meunier, F. 1907. Monographie des Dolichopodidae de l'ambre de la Baltique. *Naturaliste*, 29: 29-30.

Meunier, F. 1908a. Les Asilidae de l'ambre de la Baltique. *Bull. Soc. Entomol. France*, 2: 18-20.

Meunier, F. 1908b. Monographie des Empidae de l'ambre de la Baltique et catalogue bibliographique complet sur les diptères de cette résine. *Ann. Sci. Nat. Zool.*, (2/3), 9: 81-135.

Meunier, F. 1909. Sur quelques Diptères (Xylophagidae, Therevidae, Arthropidae, Stratiomyiidae, Tanypezinae et Ortalinae) de l'ambre de la Baltique. *Ann. Soc. Sci. Bruxelles*, 32: 258-266.

Meunier, F. 1912. Coup d'oil rètrospectif sur des Diptères succin de la Baltique. *Ann. Soc. Sci. Bruxelles*, 36: 160-186.

Meunier, F. 1914. Une blattide et une larve d'odonates du Kimméridgien de la Sierra del Montsech, Lérida (Espagne). *Mem. Real Acad. Cien. Artes Barcelona*, 11: 124-126, pls. 1-2.

Mey, W. 1985. Die Köcherfliegen des Sächsischen Bernsteins (I) (Trichoptera). *Deut. Entomol. Z.*, N.F., 32: 275-278.

Mey, W. 1986. Die Köcherfliegen des Sächsischen Bernsteins (II) (Trichoptera). *Deut. Entomol. Z.*, N.F., 33: 241-248.

Mey, W. 1988. Die Köcherfliegen des Sächsischen Bernsteins (III) (Trichoptera). *Deut. Entomol. Z.*, N.F., 35: 299-309.

Meyrick, E. 1906. On the genus *Imma* (=Tortricomorpha, Feld.). *Trans. Entomol. Soc. London*, 1906: 169-206.

Miall, L.C. and Hammond, A.R. 1892. The development of the head of the imago of *Chironomus*. *Trans. Linn. Soc. London*, 5: 265-279, pls. 28-31.

Michener, C.D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bull. Am. Mus. Nat. Hist.*, 82: 155-301.

Michener, C.D. 1952. The Saturniidae (Lepidoptera) of the Western Hemisphere. Morphology, phylogeny, and classification. *Bull. Am. Mus. Nat. Hist.*, 98: 341-501.

Michener, C.D. 1953. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. *Univ. Kansas Sci. Bull.*, 35: 987-1101.

Michener, C.D. 1979. Biogeography of the bees. *Ann. Missouri Bot. Gard.*, 66: 277-347.

Michener, C.D. and Greenberg, L. 1980. Ctenoplectridae and the origin of long-tongued bees. *Zool. J. Linn. Soc.*, 69: 183-203.

Michener, C.D. and Grimaldi, D.A. 1988a. A *Trigona* from Late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Melponinae). *Am. Mus. Novit.*, 2917: 1-10.

Michener, C.D. and Grimaldi, D.A. 1988b. The oldest fossil bee: apoid history, evolutionary stasis, and antiquity of social behavior. *Proc. Natl. Acad. Sci. USA*, 85: 6424-6426.

Mickoleit, E. 1963. Untersuchungen zur Kopfmorphologie der Thysanopteren. *Zool. Jb. (Anat.)*, 81: 101-150.

Middleton, W. 1917. Notes on the larvae of some Cephidae. *Proc. Entomol. Soc. Washington*, 19: 174-179.

Miles, P.W. 1987. Feeding process of Aphidoidea in relation to effects on their food plants. IN: Minks, A.K. and Harrewijn, P., (Eds.), *Aphids: Their Biology, Natural Enemies and Control*, A: 321-339. Amsterdam: Elsevier

Miles, P.W., McLean, D.L. and Kinsey, M.G. 1964. Evidence that two species of aphid ingest food through an open stylet sheath. *Experientia*, 20: 582.

Miller, D. 1932. The buccopharyngeal mechanism of a blow larva (*Calliphora quadrimaculata* Swed.). *Parasitology*, 24: 491-499.

Miller, F.W. 1933. Musculature of the lacewing (*Chrysopa plorabunda*) Neuroptera. *J. Morphol.*, 55: 29-51.

Miller, J.Y. 1971. The head capsule of selected Hesperioidea. *J. Res. Lepid.*, 9: 193-214.

Miller, N.C.E. 1955. The rostrum of *Centrocnemis* Signoret 1852. *Nature*, 175: 641-642.

Mills, J.S., White, R. and Gough, L.J. 1985. The chemical composition of Baltic amber. *Chem. Geol.*, 47: 15-39.

Milne, L. and Milne, M. 1980. *The Audobon Society Field Guide to North American Insects and Spiders*. New York: Alfred A. Knopf. 989 pp.

Mimura, K., Tateda, H., Morita, H. and Kuwabara, M. 1969. Regulation of insect brain excitability by ocellus. *Z. Vergl. Physiol.*, 32: 422-463.

Mitchell, P. and Wighton, D. 1979. Larval and adult insects from the Paleocene of Alberta, Canada. *Can. Entomol.*, 111: 777-782.

Mitter, C., Farrell, B. and Wiegmann, B. 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *Am. Nat.*, 132: 107-128.

Mitter, J.L. 1918. Note on the method of feeding of *Corizoneura* (*Pangonia*) *longirostris* Hardwick, with a description of the mouth parts. *Indian J. Med. Res.*, 5: 523-528.

Mittler, T.E. 1957. Studies on the feeding and nutrition of *Tuberolachnus salignus* (Gmelin) (Homoptera, Aphididae). I. The uptake of phloem sap. *J. Exp. Biol.*, 34: 334-341.

Mittler, T.E. 1958. Studies on the feeding and nutrition of *Tuberolachnus salignus* (Gmelin) (Homoptera, Aphididae). II. The nitrogen and sugar composition of ingested phloem sap and excreted honeydew. *J. Exp. Biol.*, 35: 74-84.

Miyake, T. 1912. The life historyi of *Panorpa klugi* McLachlan. *Tokyo J. Coll. Agr.*, 4: 117-139.

Mockford, E.L. 1965. The genus *Caecilius* (Psocoptera: Caecilidae). Part 1. Species groups and the North American species of the *Flavidus* Group. *Trans. Am. Entomol. Soc.*, 91: 121-166.

Mockford, E.L. 1969. Fossil insects of the order Psocoptera from Tertiary amber of Chiapas, Mexico. *J. Paleontol.*, 43: 1267-1273.

Modder, W.W.D. 1969. The mode of feeding in the silverfish *Acrotelsa collaris* (F.) (Thysanura: Lepismatidae). *Entomologist*, 102: 129-132.

Moffett, M.W. 1985. Revision of the genus *Myrmoteras* (Hymenoptera: Formicidae). *Bull. Mus. Comp. Zool.*, 151: 1-53.

Monaco, R., Parenzan, P. and Triggiani, O. 1977. L'*Euxoa temera* Hb. (Lepidoptera-Noctuidae) dannosa in Puglia. *Entomologica*, 13: 165-181.

Monros, F. 1959. *Los Generos de Chrysomelidae (Coleoptera)*. Tucuman: Univ. Nac. Tucuman. 336 p., 3 pls.

Moore, J.C. 1988. The influence of microarthropods on symbiotic and non-symbiotic mutualism in detrital based belowground food webs. *Agricult., Ecosyst., Environ.*, 24: 147-159.

Moran, N.A. 1989. A 48-million-year-old aphid--host plant association and complex life cycle: biogeographic evidence. *Science*, 245: 173-175.

Moran, V.C. and Southwood, T.R.E. 1982. The guild composition of arthropod communities in trees. *J. Anim. Ecol.*, 51: 289-306.

Mordvilko, A. 1934. On the evolution of aphids. *Arch. Naturges.*, N.F., 3: 1-60.

Morgan, A.H. 1913. A contribution to the biology of the mayflies. *Ann. Entomol. Soc. Am.*, 6: 371-413.

Morge, G. 1973. Entomology in the Western World in antiquity and medieval times. IN: Smith, R.F., Mittler, T.E. and Smith, C.N., (Eds.), *History of Entomology*, pp. 37-80. Palo Alto, CA: Annual Reviews, Inc.

Morimoto, K. 1962. Comparative morphology and phylogeny of the superfamily Curculionidea of Japan (Comparative morphology, phylogeny and systematics of the superfamily Curculionidea of Japan I). *J. Fac. Agr. Kyushu Univ.*, 11: 331-373.

Moritz, G. 1989. Die Ontogenese der Thysanoptera (Insecta) unter besonderer Berücksichtigung des Fransenflüglers *Hercinothrips femoralis* (O.M. Reuter, 1891) (Thysanoptera, Thripidae, Panchaetothripinae). IV. Mitteilung: Imago-Kopf. *Zool. Jb. (Anat.)*, 118: 273-307.

Morse, J.C. and Holzenthal, R.W. 1984. Trichoptera genera. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 312-347. Dubuque: Kendall/Hunt Publishing Co.

Morse, M. 1931. The external morphology of *Chrysopa perla* L. (Neuroptera: Chrysopidae). *J. New York Entomol. Soc.*, 39: 1-43.

Mosely, M.E. 1936. Tasmanian Trichoptera or caddis-flies. *Proc. Zool. Soc. London*, 1936: 395-431.

Mosher, E. 1915. Homology of the mouth-parts of the preimago in the Lepidoptera. *J. Entomol. Zool.*, 7: 98-106.

Motschulsky, V. 1856. Lettre a Mènètriès No. 4. *Etud. Entomol.*, 5: 21-38.

Moulins, M. 1959. Contribution a la connaissance de quelques types larvaires d'Hydrophilidae (Coleopteres). *Trav. Lab. Zool., Univ. Dijon*, 30: 1-46, figs. 1-42.

Moulins, M. 1968. Contribution a la conaissance anatomique des plecoptèrés: la region cephalique de la larve de *Nemoura cinera* Nemouridae). *Ann. Soc. Entomol. France*, N.S., 4: 91-143.

Moulins, M. 1969. Etude anatomique de l'hypopharynx de *Forficula auricularia* L. (Insecte, Dermaptere): teguments, musculature, organes sensoriels et innervations. Interpretation morphologique. *Zool. Jb. (Anat.)*, 86: 1-27.

Moulins, M. 1971. Le cavité préorale de *Blabera cranifera* Burm. (Insecta, Dictyoptère) et son innervation: étude anatomohistologique de l'èpipharynx et l'hypopharynx. *Zool. Jb. (Anat.)*, 88: 527-586.

Mound, L.A. 1970. Convoluted maxillary stylets and the systematics of some phlaeothripine Thysanoptera from *Casuarina* trees in Australia. *Aust. J. Zool.*, 18: 439-463.

Mound, L.A. 1971. The feeding apparatus of thrips. *Bull. Entomol. Res.*, 60: 547-548.

Mound, L.A., Heming, B.S. and Palmer, J.M. 1980. Phylogenetic relationships between the families of recent Thysanoptera (Insecta). *Zool. J. Linn. Soc.*, **69**: 111-141.

Mound, L.A. and O'Neill, K. 1974. Taxonomy of Merothripidae with ecological and phylogenetic considerations (Thysanoptera). *J. Nat. Hist.*, **8**: 481-509.

Muesebeck, C.F.W. 1963. A new ceraphronid from Cretaceous amber (Hymenoptera: Proctotrupoidea). *J. Paleontol.*, **37**: 129-130, pl. 17.

Muh, C. 1985. Kopfmorphologie der Larven der Tanypodinae (Chironomidae, Diptera) am Beispiel von *Macropelopia nebulosa* (Meigen). *Zool. Jb. (Anat.)*, **113**: 331-362.

Muir, F. 1925. Reconsideration of some points in the morphology of the head of Homoptera. *Ann. Entomol. Soc. Am.*, **18**: 67-73.

Muir, F. 1929. The tentorium of the Hemiptera considered from the point of view of the recent work of Snodgrass. *Entomol. Mon. Mag.*, **65**: 86-88.

Muir, F. 1931. A criticism of Dr. Hansen's theory of the maxillulae in Hemiptera. *Entomol. Mon. Mag.*, **67**: 51-53.

Muir, F. and Kershaw, J.C. 1911. On the homologies and mechanism of the mouth-parts of Hemiptera. *Psyche*, **18**: 1-12.

Muir, F. and Kershaw, J.C. 1912. The development of the mouth-parts in the Homoptera, with observations on the embryo of *Siphanta*. *Psyche*, **19**: 77-89.

Mukerji, D. and Sen-Sarma, P. 1955. Anatomy and affinity of the elephant louse, *Haematomyzus elephantis* Piaget (Insecta: Rhynchophthiraptera). *Parasitology*, **45**: 5-30.

Mulkern, G.B. 1967. Food selection by grasshoppers. *Ann. Rev. Entomol.*, **12**: 59-78.

Müller, A.H. 1975. Zur entomofauna des Permokarbon: 1. Mylacridae (Blattodea) aus dem Unterrotliegenden (Unterperm, Autun) von Thuringen. *Z. Geol. Wiss.*, **3**: 621-641.

Müller, A.H. 1978. Entomofauna des Permo-Karbon, Teil 3: Uber die Morphologie, Taxonomie und Okologie von *Eugereon boeckingi* (Palaeodictyoptera). *Freib. Forsch.*, (C), **334**: 7-20.

Müller, A.H. 1982. Uber Hyponome fossiler und rezenter Insekten, erster Beitrag. *Freib. Forsch.*, (C), **366**: 7-27, pls. 1-8.

Müller, H. 1873. *Die Befruchtung der Blumen durch Insekten*. Leipzig: Engelmann. 479 pp.

Muñiz, R. and Barrera, A. 1969. *Rhopalotria dimidiata* Chevrolat, 1878: estudio morfologico del adulto y descripcion de la larva (Ins. Col. Curcul.: Oxycoryninae). *Rev. Soc. Mex. Hist. Nat.*, 30: 205-222.

Munroe, E.G. 1982. Lepidoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 612-651. New York: McGraw-Hill Book Co.

Munscheid, L. 1933. Die Metamorphose des Labiums der Odonaten. *Z. Wiss. Zool.*, 143: 201-240.

Muralirangan, M.C. and Muralirangan, M. 1985. Physicochemical factors in the acridid feeding behaviour (Orthoptera: Acrididae). *Proc. Indian Acad. Sci. (Anim. Sci.)*, 94: 283-294.

Murphy, H.E. 1922. Notes of the biology of some of our North American species of may-flies. I. The metamorphosis of may-fly mouth parts. *Bull. Lloyd Libr., Entomol. Ser.*, 2: 1-39.

Murray, M.D. 1979. Louse ecology. IN: Kim, K.C., (Ed.), *Anoplura of the World*, pp.

Murray, M.D., Smith, M.S.R. and Soucek, Z. 1965. Studies on the ecto-parasites of seals and penguins. I. The ecology of the louse *Lepidophthirus macrorhini* Enderlein on the southern elephant seal, *Mirounga leonina* (L.). *Aust. J. Zool.*, 13: 761-771.

Murti, B.K. 1929. The suctorial apparatus of cicada. *Mysore Univ. Half-Yearly J.*, 3: 12-55

Mutuura, A. 1971. A new genus of a homoneurous moth and the description of a new species (Lepidoptera: Neopseustidae). *Can. Entomol.*, 103: 1129-1136.

Myers, J.G. 1924. On the systematic position of the family Termitiaphididae (Hemiptera, Heteroptera) with a description of a new genus and species from Panama. *Psyche*, 31: 259-278.

Narayanan, E.S., Rao, B.R.S. and Thakare, K.R. 1955. A note on differences in the structure of mandibles in ecto- and endo-parasite larvae and their relationship with their hosts. *Indian J. Entomol.*, 17: 383-385.

Naumann, C.M. 1987. On the phylogenetic significance of two Miocene zygaenid moths (Insecta, Lepidoptera). *Paläont. Z.*, 61: 299-308.

Naumann, F. 1937. Zur Reduktion des Saugrussels bei Lepidopteren und deren Beziehung zur Flugelreduktion. *Zool. Jb. (Syst).*, 70: 381-420.

Navas, L. 1914. Insectos neuropteros fosiles nuevos. *Assn. España Prog. Cien. Congr. Madrid*, 5: 35-38.

Neboiss, A. 1978a. Atriplectididae, a new caddisfly family (Trichoptera: Atriplectididae). *Proc. Second Int. Symp. Trichoptera*, pp. 67-73.

Neboiss, A. 1978b. A taxonomic and zoogeographic study of Tasmanian caddis-flies (Insecta: Trichoptera). *Mem. Natl Mus. Victoria*, 38: 1-208.

Nedel, J.O. 1960. Morphologie und Physiologie der Mandibeldruse einiger Bienen-arten (Apidae). *Z. Morphol. Okol. Tiere*, 49: 139-183.

Needham, J.G., Frost, S.W. and Tothill, B.H. 1928. *Leaf-Mining Insects*. Baltimore: Williams & Wilkins Company. 351 p.

Needham, J.G., Traver, J.R. and Hsu, Y.-C. 1935. *The Biology of May-flies, with a Systematic Account of North American Species*. Ithaca, N.Y.: Comstock Publishing Company. 759 p.

Negrobov, O.P. 1978. Flies of the superfamily Empididoidea (Diptera) from Cretaceous retinite in northern Siberia. *Paleontol. J.*, 1978(2): 221-228.

Neiswander, C.R. 1926. On the anatomy of the head and thorax in *Ranatra* (Heteroptera). *Trans. Am. Entomol. Soc.*, 51: 311-320.

Nel, A. and De Villiers, W.M., 1988. Mouthpart structure in adult scarab beetles (Coleoptera: Scarabaeoidea). *Entomol. Gen.*, 13: 95-114.

Nelson, J.A. 1924. Morphology of the honeybee larva. *J. Agr. Res.*, 28: 1167-1213, pls. 1-8.

Nelson, W.A. 1955. Artificial feeding of certain ectoparasites through membranes. *J. Parasitol.*, 41: 635-636.

Nelson, W.A., Clifford, C.M., Bell, J.F. and Hestekin, B. 1972. *Polyplax sertata*: histopathology of the skin of louse-infested mice. *Exp. Parasitol.*, 31: 194-202.

Nelson, W.A. and Petrunia, R. 1969. *Melophagus ovinus*: feeding mechanism on transilluminated mouse ear. *Exp. Parasitol.*, 26: 308-313.

Nenjukov, D.V. 1927. On some peculiarities in the nutrition of Lepidoptera [in Russian]. *La Defense des Plantes*, 4: 12-14.

New, T.R. 1987. Biology of the Psocoptera. *Orien. Ins.*, 21: 1-109.

Newcomer, E.J. 1918. Some stoneflies injurious to vegetation. *J. Agr. Res.*, 13: 37-42.

Newcomer, W.S. 1948. Embryological development of the mouth parts and related structures of the milkweed bug, *Oncopeltus fasciatus* (Dallas). *J. Morphol.*, 82: 365-411.

Newson, H.D. 1984. Culicidae. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 515-533. Dubuque, IA: Kendall/Hunt Publ. Co.

Nicholson, H.P. 1945. The morphology of the mouthparts of the non-biting blackfly, *Eusimilium dacotense* D. & S., as compared with those of the biting species, *Simulium venustum* Say (Diptera: Simuliidae). *Ann. Entomol. Soc. Am.*, 38: 281-297.

Nielsen, E.S. 1978. On the systematic position of the genus *Eriocottis* Zeller, 1847, with remarks on the phylogeny of primitive Tineoidea (Lepidoptera). *Entomol. Scand.*, 9: 279-296.

Nielsen, E.S. 1985. Primitive (non-ditrysan) Lepidoptera of the Andes: diversity, distribution, biology and phylogenetic relationships. *J. Res. Lepid., Suppl.*, 1: 1-16.

Nielsen, E.S. 1987. The recently discovered primitive (nonditrysan) Family Palaephatidae (Lepidoptera) in Australia. *Invert. Taxon*, 1: 201-229.

Nielsen, E.S. and Scoble, M.J. 1986. *Afrotheora*, a new genus of primitive Hepialidae from Africa (Lepidoptera: Hepialoidea). *Entomol. Scand.*, 17: 29-54.

Nielson, B.D. 1971. Some observations on biting midges attacking grazing cattle in Denmark. *Entomol. Scand.*, 2: 95-98.

Niklas, K.J. 1986. Large-scale changes in animal and plant terrestrial communities. IN: Raup, D.M. and Jablonski, D., (Eds.), *Patterns and Processes in the History of Life*, pp. 383-405. Berlin: Springer-Verlag.

Nilsson, L.A., Jonsson, L., Rason, L. and Randrianjohany, E. 1985. Monophyly and pollination mechanisms in *Angraecum arachnites* Schltr. (Orchidaceae) in a guild of long-tongued hawk-moths (Sphingidae) in Madagascar. *Biol. J. Linn. Soc.*, 26: 1-19.

Nilsson, L.A., Jonsson, L., Rason, L. and Randrianjohany, E. 1987. Angraecoid orchids and hawkmoths in central Madagascar: specialized pollination systems and generalist foragers. *Biotropica*, 19: 310-318.

Ninniger, H.H. 1915. Note on the mouthparts of Orthoptera. *Psyche*, 22: 13-16.

Nitrikin, L.M. 1977. Infraorder Scarabaaeiformia. IN: Arnoldi, L.V., Zherikin, V.V., Nitrikin, L.V. and Ponomarenko, A.G., "Mesozoic Coleoptera." *Trans. Paleontol. Inst.*, 161: 119-130.

Nitzulescu, V. 1926a. Sur l'armature buccale des tabanides. *C.R. Soc. Biol., Paris*, 95: 1152-1154.

Nitzulescu, V. 1926b. Contribution a l'etude de l'appareil buccal des simulides. *C.R. Soc. Biol., Paris*, 95: 1336-1338.

Nitzulescu, V. 1927a. L'appareil buccal de *Corizoneura schwetzi* et *C. inornata*. *Rev. Zool. Afr.*, 15: 125-142.

Nitzulescu, V. 1927b. Sur le stylet median de l'appareil buccal de la puce. *Bull. Soc. Path. Exot.*, 20: 467-473.

Noars, R. 1956. Contribution a la connaissance de la larve d'*Orechtochilus villosus* Mull. *Trav. Lab. Zool., Univ. Dijon*, 17: 1-32.

Norstog, K. 1987. Cycads and the origin of insect pollination. *Am. Sci.*, 75: 270-279.

Norstog, K.J., Stevenson, D.W. and Niklas, K.J. 1986. The role of beetles in the pollination of *Zamia furfuracea* L. fil. (Zamiaceae). *Biotropica*, 18: 300-306.

Northrop, R.B. 1975. Information processing in the insect compound eye. IN: Horridge, G.A., (Ed.), *The Compound Eye and Vision of Insects*, pp. 378-409. Oxford: Oxford University Press.

Northrop, S.A. 1928. Beetles from the Fox Hills Cretaceous strata of South Dakota. *Am. J. Sci.*, (5) 15: 28-38.

Norton, R.A., Bonamo, P.M., Grierson, J.D. and Shear, W.A. 1988. Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York. *J. Paleontol.*, 62: 259-269.

Nuttall, G.H.F. and Shipley, A.E. 1901. The structure and biology of *Anopheles*. The egg and larva. *J. Hyg.*, 1: 45-77.

Okada, T. 1963. Caenogenetic differentiation of mouth hooks in drosophilid larvae. *Evolution*, 17: 84-98.

Oldroyd, H. 1965. *The Natural History of Flies.* New York: W.W. Norton and Company. 324 pp.

Olfers, E.W.M. 1908. Die "Ur-Insekten" (Thysanura und Collembolen im Bernstein). *Schrift. Physik.-Okon. Ges. Konigsberg*, 48: 1-40.

Olfers, E.W.M. 1911. Ein neuer Thysanur im Bernstein. *Berl. Entomol. Z.*, 56: 151-152.

Oliver, D.R. 1981. Chironomidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 423-458.

Olsen, P.E., Remington, C.L., Cornet, B. and Thomson, K.S. 1978. Cyclic change in Late Triassic communities. *Science*, 201: 729-733.

O'Meara, G.F. 1987. Nutritional ecology of blood-feeding Diptera. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 741-764. New York: John Wiley and Sons.

Opler, P.A. 1973. Fossil lepidopterous leaf mines demonstrate the age of some insect-plant relationships. *Science*, 179: 1321-1323.

Osten, T. 1982. Vergleichend-funktionsmorphologische Untersuchungen der Kopfkapsel und der Mundwerkzeuge ausgewählter "Scolioidea" (Hymenoptera, Aculeata). *Stutt. Beit. Naturk.*, (A), 354: 1-60.

Osterwald, T. 1954. Beobachtungen uber die Nahrungsaunahme des Maikafers und eine Untersuchung seiner Mundwerkzeuge. *Mikrokosmos*, 43: 186-188.

Otanes, F.Q. 1922. Head and mouth-parts of Mecoptera. *Ann. Entomol. Soc. Am.*, 15: 310-323.

O'Toole, C., (Ed.) 1986. *The Encyclopedia of Insects.* New York: Facts on File, Inc. 152 p.

Otter, G.W. 1938. On the morphology of the larvae of three species of Cecidomyiidae (Diptera) from knapweed (*Centaurea*) flowers. *Trans. Roy. Entomol. Soc. London*, 87: 39-68.

Ottosson, J.G. and Anderson, J.M. 1983. Number, seasonality and feeding habits of insects attacking ferns in Britain: an ecological consideration. *J. Anim. Ecol.*, 52: 385-406.

Owen, D.F. and Wiegert, R.G. 1987. Leaf eating as mutualism. IN: Barbosa, P. and Schultz, J.C., (Eds.), *Insect Outbreaks*, pp. 81-95. New York: Academic Press, Inc.

Owen, J. 1980. *Feeding Strategy*. Chicago: University of Chicago Press. 160 p.

Pace, R. 1985. Uno straordinario mirmecofilo: *Loeblius nepalensis* gen. et sp. nov. (Coleoptera Staphylinidae). *Revue Suisse Zool.*, 92: 291-297.

Packard, A.S. 1889. On the occurrence of organs probably of taste in the epipharynx of the Mecaptera (*Panorpa* and *Boreus*). *Psyche*, 5: 159-164.

Packard, A.S. 1895. On a new classification of the Lepidoptera. *Am. Nat.*, 29: 636-647, 788-803.

Packard, A.S. 1898. The head and its appendages. IN: Packard, A.S., *A Text-Book of Entomology, Including the Anatomy, Physiology, Embryology and Metamorphoses of Insects*, pp. 42-85. London: Macmillan and Company.

Paclt, J. 1972. Grundsätzliches zur chorologie und Systematik der Felsenspringer. *Zool. Anz.*, 188: 422-429.

Pajni, H.R. and Chhibba, K.K. 1972. Structure of rostrum in *Calandra oryzae* (L.) (Coleoptera: Curculionidae). *Int. J. Insect Morphol. Embryol.*, 1: 219-223.

Pakaluk, J. 1987. Revision and phylogeny of the Neotropical genus *Hoplicnema* Matthews (Coleoptera: Corylophidae). *Trans. Am. Entomol. Soc.*, 113: 73-116.

Palmer, A.R. 1957. Miocene arthropods from the Mojave Desert, California. *U.S. Geol. Surv. Prof. Pap.*, 294-G: 237-280, pls. 1-5.

Palmer, W.A. 1987. The phytophagous insect fauna associated with *Baccharis halimifolia* L. and *B. neglecta* Britton in Texas, Louisiana, and northern Mexico. *Proc. Entomol. Soc. Washington*, 89: 185-199.

Panfilov, D.V. 1968. Kalligrammatids (Neuroptera, Kalligrammatidae) from the Jurassic deposits of Karatau. IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 166-174. Moscow: Academy of Sciences. [In Russian.]

Pao, B. and Knight, K.L. 1970. Morphology of the fourth stage larval mouthparts of *Aedes* (*Aedimorphus*) *vexans* (Diptera: Culicidae). *J. Georgia Entomol. Soc.*, 5: 115-137.

Paramonov, S.J. 1950. A review of the Australian Mydaidae (Diptera). *Bull. Commonw. Sci. Indust. Res. Org.*, 255: 1-32.

Paranjape, S.Y. 1985. Behavioural analysis of feeding and breeding in orthopterid insects. *Proc. Indian Acad. Sci. (Anim. Sci.)*, 94: 265-282.

Park, O. 1942. A study in neotropical Pselaphidae. *Northwestern Univ. Stud. Biol. Sci. Med.*, 1: 1-403, pls. 1-21.

Parker, D.E. 1936. *Chrysis shanghaiensis* Smith, a parasite of the oriental moth. *J. Agr. Res.*, 52: 449-458.

Parker, H.L. 1943. Gross anatomy of the larva of the wasp *Polistes gallicus* (L.) (Hymenoptera, Vespidae). *Ann. Entomol. Soc. Am.*, 36: 619-624.

Parker, H.L. and Smith, H.D. 1933. Additional notes on the strepsipteron *Eoxenos laboulbenei* Peyerimhoff. *Ann. Entomol. Soc. Am.*, 26: 217-231, pls. 1-2.

Parker, H.L. and Thompson, W.R. 1925. Notes on the larvae of the Chalcidoidea. *Ann. Entomol. Soc. Am.*, 18: 384-395, pls. 26-28.

Parker, S.P, (Ed.) 1982 *Synopsis and Classification of Living Organisms*, 2 vols. New York: McGraw-Hill Book Co. 1166 + 1232 p.

Parrish, W.B. 1967. The origin, morphology, and innervation of aphid stylets (Homoptera). *Ann. Entomol. Soc. Am.*, 60: 273-276.

Parsons, M.C. 1958. Cephalic glands in *Gelastocoris* (Hemiptera Heteroptera). *Psyche*, 65: 99-107.

Parsons, M.C. 1959. Skeleton and musculature of the head of *Gelastocoris oculatus* (Fabricus) (Hemiptera Heteroptera). *Bull. Mus. Comp. Zool.*, 122:-353.

Parsons, M.C. 1962. Skeleton and musculature of the head of *Saldula pallipes* (F.) (Heteroptera: Saldidae). *Trans. Roy. Entomol. Soc.*, 114: 97-130.

Parsons, M.C. 1963. The endoskeletal salivary pumping apparatus in representative Belostomatidae (Heteroptera). *Can. J. Zool.*, 41: 1017-1024.

Parsons, M.C. 1964a. The salivary pumping apparatus of Belostomatidae (Heteroptera). *Can. Entomol.*, 96: 141.

Parsons, M.C. 1964b. The origin and development of the hemipteran cranium. *Can. J. Zool.*, 42: 409-432.

Parsons, M.C. 1965a. Cranial development in the Hemiptera. *Trans. 12th Int. Congr. Entomol.*, 1: 135.

Parsons, M.C. 1965b. Clypeal modification in some littoral and aquatic Heteroptera. *Can. J. Zool.*, 43: 161-166.

Parsons, M.C. 1966a. Modifications of the food pumps of Hydrocorisae (Heteroptera). *Can. J. Zool.*, 44: 585-620.

Parsons, M.C. 1966b. Labial skeleton and musculature of the Hydrocorisae (Heteroptera). *Can. J. Zool.*, 44: 1051-1084.

Parsons, M.C. 1966c. Studies on the cephalic anatomy of Naucoridae (Heteroptera). *Trans. Roy Entomol. Soc. London*, **118**: 119-151.

Parsons, M.C. 1968. The cephalic and prothoracic skeleto-musculature and nervous system in *Lethocerus* (Heteroptera, Belostomatidae). *J. Linn. Soc. (Zool.)*, 47: 349-406.

Parsons, M.C. 1969a. The labium of *Aphelocheirus aestivalis* F. as compared with that of typical Naucoridae (Heteroptera). *Can. J. Zool.*, 47: 295-306.

Parsons, M.C. 1969b. The food pump of *Aphelocheirus aestivalis* F. as compared with that of typical Naucoridae (Heteroptera). *J. Morphol.*, **129**: 17-30.

Parsons, M.C. 1972. Fine structure of the triturating devices in the food pump of *Notonecta* (Heteroptera, Notonectidae). *J. Morphol.*, 138: 141-168.

Patterson, B.D. 1983. Grasshopper mandibles and the niche variation hypothesis. *Evolution*, 37: 375-388.

Patterson, B.D. 1984. Correlation between mandibular morphology and specific diet of some desert grassland Acrididae (Orthoptera). *Am. Midl. Nat.*, 111: 296-303.

Patton, W.S. 1933. Studies on the higher Diptera of medical and veterinary importance. A revision of the genera of the Tribe Muscini, Subfamily Muscinae based on a comparative study of the male terminalia. 1. The genus *Musca* Linneaus. *Ann. Trop. Med. Parasitol.*, 27: 135-156.

Patton, W.S. and Cragg, F.W. 1913. *A Textbook of Medical Entomology.* London: Christian Literature Society for India. 768 p.

Paulus, H.F. 1974. Die phylogenetische Bedeutung der Ommatidien der apterygoten Insekten (Collembola, Archaeognatha und Zygentoma). *Pedobiologia*, 14: 123-133.

Pauly, M. 1915. Die Mundwerkzeuge der Caraboidea. *Arch. Naturges.*, (A), 81: 1-101.

Pavlovsky, E.N. 1922. The biology and structure of the larvae of *Hydrophilus caraboides* L. *Quart. J. Micros. Sci.*, **66**: 627-655.

Payne, J.A. 1965. A summer carrion study of the baby pig (*Sus scrofa*). *Ecology*, **46**: 592-602.

Paysinger, J.T., Noblet, R., Adkins, T.R., Jr. and Vaughn, E.A. 1978. Scanning electron microscopy of the adult mouthparts of the horn fly and the face fly. *J. Georgia Entomol. Soc.*, **13**: 28-39.

Peacock, A.D. 1919. The structure of the mouthparts and mechanism of feeding in *Pediculus humanus*. *Parasitology*, **11**: 98-117.

Pearman, J.V. 1928. Biological observations on British Psocoptera. *Entomol. Month Mag.*, **64**: 263-268.

Pearson, D., 1988. What is the adaptive significance of multicomponent defensive repertoires? *Proc. 18th Int. Congr. Entomol.*, **1988**: 204. [Oral presentation during 4 July 1988.]

Pechuman, L.L. and Teskey, H.J. 1981. Tabanidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 463-478.

Peel, A.J. 1975. Investigations with aphid stylets into the physiology of the sieve tube. IN: Zimmermann, M.H. and Milburn, J.A., (Eds.), *Transport in Plants. I. Phloem Transport*, pp. 171-195. Berlin: Springer-Verlag.

Pellmyr, O. and Thien, L.B. 1986. Insect reproduction and floral fragrances: keys to the evolution of the angiosperms? *Taxon*, **35**: 76-85.

Penny, N.D. and Arias, J.R. 1982. *Insects of an Amazon Forest*. New York: Columbia Univ. Press. 269 p.

Perfiljew, P.P. 1927. Zur Anatomie der Flohlarven. *Z. Morphol. Okol. Tiere*, **7**: 102-126.

Perraudin, J. 1961. Recherches sur l'anatomie cephalique des larves de bibionides et de lycoriides (Dipt. Nematocera). *Trav. Lab. Zool., Univ. Dijon*, **41**: 1-47.

Peschke, K., Krapf, D. and Fuldner, D. 1987. Ecological separation, functional relationships, and limiting resources in a carrion insect community. *Zool. Jb. (Syst.)*, **114**: 241-265.

Pesson, P. 1944. *Contribution à l'Etude Morphologique et Fonctionnelle de la Tête, de l'Appareil Buccal et du Tube Digéstif de la Femelle de Coccides*. Paris: Monographes Station et Laboratoire de Recherché Agronomique. 226 p.

Peters, T.M. 1981. Dixidae. IN: McAlpine, J.F., et al., "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 329-334.

Peterson, A. 1912. Anatomy of the tomato-worm larva, *Protoparce carolina*. *Ann. Entomol. Soc. Am.*, 5: 246-269.

Peterson, A. 1915. Morphological studies on the head and mouth-parts of the Thysanoptera. *Ann. Entomol. Soc. Am.*, 8: 20-59.

Peterson, A. 1916. The head-capsule and mouth-parts of Diptera. *Illinois Biol. Mon.*, 3: 1-113.

Peterson, A. 1948. *Larvae of Insects: An Introduction to Nearctic Species. Part I. Lepidoptera and Plant Infesting Hymenoptera.* Ann Arbor, MI: Edwards Brothers, Inc. 315 p.

Peterson, A. 1951. *Larvae of Insects: An Introduction to Nearctic Species. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera.* Ann Arbor, MI: Edwards Brothers, Inc. 416 p.

Peterson, B.V. 1975. A new Cretaceous bibionid from Canadian amber (Diptera: Bibionidae). *Can. Entomol.*, 107: 711-715.

Peterson, B.V. 1981a. Anisopodidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 305-312.

Peterson, B.V. 1981b. Simuliidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 355-392.

Peterson, B.V. 1981c. Apioceridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 541-548.

Peterson, B.V. 1984. Simuliidae. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 534-550. Dubuque, IA: Kendall/Hunt Publ. Co.

Peterson, B.V. 1987a. Phoridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, 28: 689-712.

Peterson, B.V. 1987b. Braulidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2: *Res. Branch Agr. Canada*, 28: 913-918.

Peterson, B.V. and Cook, E.F. 1981. Synneuridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 321-324.

Peterson, B.V. and Wenzel, R.L. 1987. Nycteribiidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, 28: 1283-1291.

Peus, F. 1968. Uber die beiden Bernstein-Flöhe (Insecta, Siphonaptera). *Palaönt. Z.*, 42: 62-72.

Philpott, A. 1925. The labial palpi of *Trichophysetis cretacea* and *Argyria amoenalis*. *Proc. Linn. Soc. New South Wales*, 50: 381-382.

Philpott, A. 1927. The maxillae in the Lepidoptera. *Trans. Proc. New Zealand Inst.*, 57: 721-746.

Picker, M.D. 1987. An unusual species of spoon-wing lacewing (Neuroptera: Nemopteridae) from South Africa, with notes on its biology. *Syst. Entomol.*, 12: 239-248.

Picquet, N. 1958. Contribution a l'etude des larves de Formicidae de la Cote-d'Or. *Trav. Lab. Zool., Univ. Dijon*, 23: 1-48, figs. 1-44.

Pictet, F.J. 1854. *Traité de Paléontologie ou Histoire Naturelle des Animaux Fossiles Considérés dans leurs Rapports Zoologiques et Geologiques. II.* Paris.

Pictet-Baraban, F.J. and Hagen, H. 1856. Die im Bernstein befindlichen Neuropteren der Vorwelt (mit Zusätzen von A. Menge). IN: Berendt, G.C., (Ed.), *Die im Bernstein Befindlichen Organischen Reste der Vorwelt II.* 2: 41-125.

Pierce, W.D. 1918. The comparative morphology of the Order Strepsiptera together with records and descriptions of insects. *Proc. U.S. Natl. Mus.*, 54: 391-501, pls. 64-78.

Pierce, W.D. 1950. Fossil arthropods from onyx marble. *Bull. So. California Acad. Sci.*, 49: 101-104.

Pierce, W.D. 1966. Fossil arthropods of California. 29. Silicified Miocene pupae of ceratopogonid flies. *Bull. So. California Acad. Sci.*, 65: 81-98.

Ping, C. 1928. Study of the Cretaceous fossil insects of China. *Palaeontol. Sinica*, (B), 13: 5-57.

Ping, C. 1935. On four fossil insects from Sinkiang. *Chin. J. Zool.*, 1: 107-115.

Pinhey, E.C.G. 1975. *Moths of Southern Africa: Descriptions and Color Illustrations of 1183 Species.* Capetown, South Africa: Talfelberg, Publishers. 273 pp.

Pinhey, E.C.G. 1982. Odonata. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 338-345. New York: McGraw-Hill Book Co.

Pirngruber, O. 1944. Blütenökologische Untersuchungen über einige Falter der Gattung *Micropteryx*. *Verhandl. Zool. Bot. Ges. Wien*, 41: 129-220.

Pirone, P.P. 1970. *Diseases and Pests of Ornamental Plants.* New York: Ronald Press Company.

Piton, L.-E. 1938. *Succinotettix chopardi* Piton, orthoptère (Tetricinae) inéid de l'ambre de la Baltique. *Bull. Soc. Entomol. France*, 43: 226-227.

Piton, L.-E. 1940. *Pal'ontologie du Gisement Eocène de Menat (Puy-de-Dôme) (Flore et Fauna).* Paris. 306 p.

Plant, J.D. and Paulus, H.F. 1987. Comparative morphology of the postmentum of bees (Hymenoptera: Apoidea) with special remarks on the evolution of the lorum. *Z. Zool. Syst. Evol.-Forsch.*, 25: 81-103.

Plateau, F. 1885. Experiences sur le role des palpes chez les arthropodes maxilles. Premiere partie. Palpes des insectes broyeurs. *Bull. Soc. Zool. France*, 10: 67-90.

Plumstead, E.P. 1963. The influence of plants and environment of the developing animal life of Karoo times. *South Afr. J. Sci.*, 59: 147-152, pls. A-B.

Poinar, G.P., Jr. 1988. *Zorotypus palaeus*, new species, a fossil Zoraptera (Insecta) in Dominican amber. *J. New York Entomol. Soc.*, 96: 253-259.

Pollard, D.G. 1955. Feeding habits of the cotton whitefly, *Bemisia tabaci* Genn. (Homoptera: Aleyrodidae). *Ann. Appl. Biol.*, 43: 664-671.

Pollard, D.G. 1959. Feeding habits of the lace-bug *Urentius aegypticus* Bergevin (Hemiptera: Tingidae). *Ann. Appl. Biol.*, 47: 778-782.

Pollard, D.G. 1969. Directional control of stylets in phytophagous Hemiptera. *Proc. Roy. Entomol. Soc. London*, (A), 44: 173-185.

Pollard, D.G. 1972. The stylet structure of a leafhopper (*Eupteryx melissae* Curtis: Homoptera, Cicadellidae). *J. Nat. Hist.*, **6**: 261-271.

Pollard, D.G. 1973. Plant penetration by feeding aphids (Hemiptera, Aphidoidea): a review. *Bull. Entomol. Res.*, **62**: 631-714.

Pollard, D.G. 1977. Aphid penetration of plant tissues. IN: Harris, K.F. and Maramorosch, K., (Eds.), *Aphids as Virus Vectors*, pp. 105-118. New York: Academic Press.

Ponomarenko, A.G. 1963. Early Jurassic water beetles from the Angara River. *Palaeontol. Zhur.*, **1963**(4): 128-131. [In Russian.]

Ponomarenko, A.G. 1969a. Historical development of the Coleoptera Archostemmata. *Trans. Paleontol. Inst.*, **125**: 1-239, pls. 1-14. Moscow: Academy of Sciences. [In Russian.]

Ponomarenko, A.G. 1969b. Cretaceous insects from Labrador. 4. A new family of beetles (Coleoptera: Archostemmata). *Psyche*, **76**: 306-310.

Ponomarenko, A.G. 1971. Systematic position of some beetles from the Solenhofen shales of Bavaria. *Paleontol. J.*, **1971**(1): 62-75.

Ponomarenko, A.G. 1973. Mesozoic whirligig beetles (Gyrinidae, Coleoptera). *Paleontol. J.*, **1973**(4): 499-506.

Ponomarenko, A.G. 1976a. Corydalidae (Megaloptera) from the Cretaceous of northern Asia. *Entomol. Rev.*, **55**: 114-122.

Ponomarenko, A.G. 1976b. A new insect from the Cretaceous of Transbaikalia, a possible parasite of pterosaurians. *Paleontol. J.*, **1976**(3): 339-343.

Ponomarenko, A.G. 1977a. Paleozoic members of the Megaloptera (Insecta). *Paleontol. J.*, **1977**(1): 73-81.

Ponomarenko, A.G. 1977b. Suborder Adephaga. IN: Arnoldi, L.V., Zherikin, V.V., Nitrikin, L.M. and Ponomarenko, A.G., "Mesozoic Coleoptera." *Trans. Paleontol. Inst.*, **161**: 17-104.

Ponomarenko, A.G. 1980. Myrmeleontidea. IN: Rohdendorf, B.B. and Rasnitsyn, A.P., (Eds.), "Historical Development of the Class Insecta." *Trans. Paleontol. Inst.*, **175**: 84-99.

Ponomarenko, A.G. 1985. Neuroptera from the Jurassic in eastern Asia. *Paleontol. J.*, **1985**(3): 59-69.

Ponomarenko, A.G. 1988a. New Mesozoic water beetles (Insecta, Coleoptera) from Asia. *Paleontol. J.*, 1988(2): 79-92.

Ponomarenko, A.G., (Ed.) 1988b. *The Mesozoic Biocoenotic Crisis in the Evolution of Insects*. Moscow: Academy of Sciences. 230 p. [In Russian.]

Ponomarenko, A.G. and Rasnitsyn, A.P. 1974. New Mesozoic and Cenozoic Protomecoptera. *Paleontol. J.*, 1974(4): 493-507.

Poole, T.B. 1959. Studies on the food of Collembola in a Douglas Fir plantation. *Proc. Zool. Soc. London*, 132: 71-82.

Popham, E.J. 1959. The anatomy in relation to the feeding habits of *Forficula auricularia* L. and other Dermaptera. *Proc. Zool. Soc. London*, 133: 251-300.

Popham, E.J. 1961. The functional morphology of the mouthparts of the cockroach *Periplaneta americana* L. *Entomologist*, 94: 185-192.

Popham, E.J. 1962a. The anatomy related to the feeding habits *Arixenia* and *Hemimerus* (Dermaptera). *Proc. Zool. Soc. London*, 139: 429-450.

Popham, E.J. 1962b. On the salivary pump of *Dysdercus intermedius* Dist. (Hemiptera Heteroptera) and other bugs. *Proc. Zool. Soc. London*, 139: 489-493.

Popham, E.J. and Abdillahi, M. 1975. Some aspects of the functional morphology of the head of *Glossina morsitans orientalis* Vanderplank (Diptera, Glossinidae). *Forma Funct.*, 8: 305-330.

Popham, E.J. and Bevans, E. 1979. Functional morphology of the feeding apparatus in larval and adult *Aeshna juncea* (L.) (Anisoptera: Aeshnidae). *Odonatologia*, 8: 301-318.

Popov, A.V. 1965. The life-cycle of the louse flies *Lipoptena cervi* L. and *Stenopteryx hirundinis* L. (Diptera, Hippoboscidae). *Entomol. Rev.*, 44: 337-343.

Popov, Y.A. 1968. The true bugs of the Jurassic fauna of Karatau (Heteroptera). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 99-113. Moscow: Academy of Sciences. [In Russian.]

Popov, Y.A. 1971. Origin and main evolutionary trends of Nepomorpha bugs. *Trans. 13th Int. Congr. Entomol.*, 1: 282-283.

Popov, Y.A. 1980. Superorder Cimicidea. IN: Rohdendorf, B.B. and Rasnitsyn, A.G., (Eds.), Historical development of the class Insecta. *Trans. Paleontol. Inst.*, 175: 58-69.

Popov, Y.A. 1982. Upper Jurassic hemipterans, genus *Olgamartynovia* (Hemiptera, Progonocimicidae) from central Asia. *Paleontol. J.*, **1982**(2): 78-94.

Popov, Y.A. 1987. A new species of the bug genus *Empicoris* Wolff from Dominican copal, with the redescription of *E. nudus* McAtee & Malloch (Heteroptera: Reduviidae: Emesinae). *Stutt. Beitr. Naturk.*, (B) **134**: 1-9.

Popov, Y.A. and Wootton, R.J. 1977. The Upper Liassic Heteroptera of Mecklenburg and Saxony. *Syst. Entomol.*, **2**: 333-351.

Porsch, O. 1958. Alte Insektentypen als Blumenausbeuter. *Oster. Bot. Z.*, **104**: 115-164.

Portier, P. 1949. La biologie des lepidopteres. IN: Lechevalier, P., (Ed.), *Encyclopedie Entomologique*, **23A**: 1-643. Paris: Jouve, Imprimeurs.

Potonié, R. 1921. Mitteilungen über mazerierte kohlige Pflanzenfossilien. *Z. Bot.*, **13**: 79-89.

Poulton, E.B. 1906. Predaceous insects and their prey. *Trans. Entomol. Soc. London*, **1906**: 323-409.

Powell, J.A. 1980. Evolution of larval food preferences in Microlepidoptera. *Ann. Rev. Entomol.*, **25**: 133-159.

Powell, J.A. and Mackie, R.A. 1966. Biological interrelationships of moths and *Yucca whipplei*. *Univ. California Publ. Entomol.*, **42**: 1-46.

Pradhan, K.S. 1950. On the head capsule, mouth-parts and related muscles of the larva of the wooly bear, *Anthrenus fasciatus* Herbst, (Coleoptera: Dermestidae). *Rec. Indian Mus.*, **46**: 73-86.

Pradhan, S. 1939a. Glands in the head capsule of coccinellid beetles with a discussion on some aspects of gnathal glands. *J. Morphol.*, **64**: 47-66.

Pradhan, S. 1939b. Neuro-muscular study of the mouth-parts of *Coccinella septempunctata*, with a comparison of the mouth-parts in carnivorous and herbivorous coccinellids. *Rec. Indian Mus.*, **40**: 341-358.

Pradhan, S. and Aren, N.S. 1941. Anatomy and musculature of the mouthparts of *Scirpophaga nivella* (Pyralidae), with a discussion on the coiling and uncoiling mechanisms of the proboscis in Lepidoptera. *Indian J. Entomol.*, **3**: 179-195.

Prasad, R.S. 1985. Behavioural analysis of feeding and reproduction in haematophagous insects. *Proc. Indian Acad. Sci. (Anim. Sci.)*, 94: 225-238.

Price, P.R. 1980. The extent of adaptive radiation in fleas. IN: Traub, R. and Starcke, H., (Eds.), *Fleas*, pp. 69-78. Rotterdam: Balkema.

Priesner, H. 1924. Bernstein-Thysanopteren. *Entomol. Mitt.*, 13: 130-151.

Priesner, H. 1929. Bernstein-Thysanopteren II. *Bernstein Forsch.*, 1: 111-138, pl. 8.

Priesner, H. and Quievreux, F. 1935. Thysanoptères des couches de potasse du Haut-Rhin. *Bull. Soc. Geol. France*, (5), 5: 471-477.

Principi, M.M. 1954. Contributi allo studio dei neurotteri Italiani. XI. *Chrysopa viridana* Schn. *Boll. Ist. Entomol., Bologna Univ.*, 20: 359-376.

Pritchard, G. 1964. The prey of dragonfly larvae (Odonata: Anisoptera) in ponds in Northern Alberta. *Can. J. Zool.*, 42: 785-800.

Pritchard, G. 1976. Further observations on the functional morphology of the head and mouthparts of dragonfly larvae (Odonata). *Quaest. Entomol.*, 12: 89-114.

Pritchard, G. and Scholefield, P. 1978. Observations on the food, feeding behaviour, and associated sense organs of *Grylloblatta campodeiformis* (Grylloblattodea). *Can. Entomol.*, 110: 205-212.

Pritykina, L.N. 1968. Dragonflies of Karatau (Odonata). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 26-54. Moscow: Academy of Sciences. [In Russian.]

Pritykina, L.N. 1970. Triassic and Jurassic dragonflies of the Liassophlebiidae from Soviet Central Asia. *Paleontol. J.*, 1970(1): 91-102.

Pritykina, L.N. 1977. New dragonflies from Lower Cretaceous deposits of Transbaikalia and Mongolia. *Trans. Mesozoic Cenozoic Faunas, Floras Biostrat. Mongolia*, 4: 81-96. pls. 1-4.

Pritykina, L.N. 1981. New Triassic dragonflies from central Asia. *Trans. Paleontol. Inst.*, 183: 5-42, pls. 1-13. [In Russian.]

Proctor, M. and Yeo, P. 1973. *The Pollination of Flowers*, 3rd rev. edn. Glasgow: William Collins Sons and Co. 418 pp.

Prota, R. 1962. Note morfo-etologiche su *Magdalis barbicornis* Latr. (Coleoptera Curculionidae). *Mem. Soc. Entomol. Ital.*, **41**: 45-66.

Pruthi, H.S. 1969. *Textbook on Agricultural Entomology*. New Delhi: Indian Council of Agricultural Research. 977 p.

Pruvost, P. 1927. Sur une aile d'insecte trouvée au sondage de Gulpen. *Jversl. Geol. Burgundie Ned Mijngeb. Heerlen*, **1926**: 76-77.

Pruvost, P. 1933. Un ancêtre des libellules dans de terrain houiller de Tchécoslovaquie. *Ann. Soc. Geol. Nord*, **58**: 149-155, pl. 5.

Pryor, M.G.M. 1948. Mouthparts and feeding habits of Blepharoceridae (Diptera). *Proc. Roy. Entomol. Soc. London*, (A), **23**: 67-70.

Pu, J. 1936. Unrecorded glands in the mouthparts of Hydrophilidae. *Peking Nat. Hist. Bull.*, **10**: 353-359.

Pucat, A.M. 1965. The functional morphology of the mouth-parts of some mosquito larvae. *Quaest. Entomol.*, **1**: 41-86.

Puchkova, L.V. 1970. The origin of the main structures of the head in the Hemiptera. *Entomol. Rev.*, **49**: 318-323.

Puri, V.D. 1957. Studies on the anatomy of the sugarcane moth borers. II. External anatomy of *Chilo tumidicostalis*, the stem borer of sugarcane. *Proc. Indian Acad. Sci., Suppl.*, (B), **45**: 196-215, pls. 8-18

Puri, V.D. 1958. Studies on the anatomy of the sugarcane moth borers. III. Comparative study of the head and its appendages. *Proc. Indian Acad. Sci., Suppl.*, (B), **46**: 96-109, pls. 8-12.

Pyke, G.H. 1978. Optimal foraging in bumblebees and coevolution with their plants. *Oecologia*, **36**: 281-293.

Pyke, M. 1981. *The Audobon Society Field Guide to North American Butterflies*. New York: Alfred A. Knopf. 924 p.

Qadri, M.A.H. 1936. Studies on the mouth-parts of Mallophaga infesting north Indian birds. *Proc. Indian Acad. Sci.*, (B), **3**: 411-423.

Qadri, M.A.H. 1949. On the digestive system and the skeletomuscular structures of the head capsule in the mangohoppers, *Idiocerus niveosparsus* (Leth.) and *Idiocerus clypealis* (Leth.) (Homoptera: Jassidae). *Proc. Zool. Soc. Bengal*, **2**: 43-55.

Qadri, M.A.H. 1951. On the anatomy of the mouth-parts and the mode of feeding in the aquatic bugs (Cryptocerata). *Proc. Zool. Soc. Bengal*, **4**: 117-135.

Qadri, M.A.H. 1959. Mechanism of feeding in Hemiptera. *Smithson. Misc. Collns.*, 137: 237-245.

Qadri, M.A.H. and Aziz, A. 1950. Biology, life-history, and external and internal anatomy of *Pyrilla perpusilla* Walker. *Algarh Muslim Univ., Zool. Ser.*, 2: 1-31.

Quate, L.W. 1961. Fossil Psychodidae (Diptera: Insecta) in Mexican amber. Part 1. *J. Paleontol.*, 37: 949-951.

Quate, L.W. 1963. Fossil Psychodidae in Mexican amber. Part 2. *J. Paleontol.*, 37: 110-118.

Quate, L.W. and Vockeroth, J.R. 1981. Psychodidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 293-300.

Quennedey, A. 1965. Contribution a la connaissance de quelques types larvaires de Sphaeridiinae (Col. Hydrophilidae). *Trav. Lab. Zool., Univ. Dijon*, 66: 1-56.

Rahle, W. 1970. Untersuchungen an Kopf und Prothorax von *Embia ramburi* Rimsky-Korsakow 1906 (Embioptera, Embiidae). *Zool. Jb. (Anat.)*, 87: 248-330.

Raj, J.S. 1943. Mouth parts of *Lamprophorus tenebrosus* Wlk. *Cur. Sci.*, 12: 83-84.

Rakshpal, R. 1954. Studies on *Gryllotalpa africana* Beauvois. *Indian J. Entomol.*, 16: 37-54.

Ramcke, J. 1965. Kopf der Schweinelaus (*Haematopinus suis* L., Anoplura). *Zool. Jb. (Anat.)*, 82: 547-663.

Randriamamonjy, F. 1963. Squelette et musculature cephaliques de *Phthorimaea heliopa* Low. (Gelechiidae, Lepidoptera). *Trav. Lab. Zool., Univ. Dijon*, 51: 1-76, figs. 1-32.

Rasnitsyn, A.P. 1963. New Late Jurassic hymenopterans from Karatau. *Paleontol. Zhur.*, 1963(1): 86-99.

Rasnitsyn, A.P. 1964. New Triassic Hymenoptera of Central Asia. *Paleontol. Zhur.*, 1964(1): 88-96. [In Russian.]

Rasnitsyn, A.P. 1968. New Mesozoic sawflies (Hymenoptera, Symphyta). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 190-236. Moscow: Academy of Sciences. [In Russian.]

Rasnitsyn, A.P. 1969. Origin and evolution of Lower Hymenoptera. *Trans. Paleontol. Inst.*, 123: 1-185, pls. 1-8. [In Russian.]

Rasnitsyn, A.P. 1972. Late Jurassic hymenopterous insects (Preaulacidae) of Karatau. *Paleontol. J.*, **1972**(1): 62-77.

Rasnitsyn, A.P. 1975. Hymenoptera Apocrita of the Mesozoic. *Trans. Paleontol. Inst.*, **147**: 1-134, pls. 1-8. [In Russian.]

Rasnitsyn, A.P. 1977a. New Hymenoptera from the Jurassic and Cretaceous of Asia. *Paleontol. J.*, **1977**(3): 349-357.

Rasnitsyn, A.P. 1977b. A new family of sawflies (Hymenoptera, Tenthredinoidea, Electrotomidae) from Baltic amber. *Zool. Zhur.*, **56**: 1304-1308. [In Russian.]

Rasnitsyn, A.P. 1980. Origin and evolution of the Hymenoptera (Insecta). *Trans. Paleontol. Inst.*, **174**: 1-191, pls. 1-3. [In Russian.]

Rasnitsyn, A.P. 1982. Triassic and Jurassic insects of the genus *Shurabia* (Grylloblattida, Geinitziidae). *Paleontol. J.*, **1982**(3): 77-86.

Rasnitsyn, A.P. 1983a. First find of a moth from the Jurassic. *Dokl. Akad. Nauk SSSR*, **269**: 467-471. [In Russian.]

Rasnitsyn, A.P. 1983b. Fossil Hymenoptera of the superfamily Pamphilioidea. *Paleontol. J.*, **1983**(2): 56-70.

Rasnitsyn, A.P. 1988. Problems in the global terrestrial biocoenotic crisis during the Middle Cretaceous Period. IN: Ponomarenko, A.G., (Ed.), *The Mesozoic Biocoenotic Crisis in the Evolution of Insects*, pp. 191-207. Moscow: Academy of Sciences. [In Russian.]

Rastogi, S.C. 1965. The food pump and associated structures in *Coridius janus* (Fabr.) (Heteroptera: Dinidoridae). *Proc. Roy. Entomol. Soc. London*, (A), **40**: 125-134.

Rathcke, B.J. 1976. Insect-plant patterns and relationships in the stem-boring guild. *Am. Midl. Nat.*, **96**: 98-117.

Rathcke, B.J. and Poole, R.W. 1974. Coevolutionary race continues: butterfly larval adaptation to plant trichomes. *Science*, **187**: 175-176.

Rathore, Y.K. 1961. Studies on the mouth-parts and feeding mechanism in *Dysdercus cingulatus* Fabr. (Pyrrhocoridae: Heteroptera). *Indian J. Entomol.*, **23**: 163-185.

Raup, D.M. and Stanley, S.M. 1978. *Principles of Paleontology*, 2nd edn. San Francisco: W.H. Freeman and Co. 481 pp.

Rayner, R.J. 1987. March flies from an African Cretaceous springtime. *Lethaea*, 20: 123-127.

Razowski, J. 1974. Phylogeny and classification of Lepidoptera. *Acta Zool. Cracovien.*, 19: 1-18.

Rebel, H. 1934. Bernstein--Lepidopteren. *Palaeobiologica*, 6: 1-16, pl. 1.

Rebel, H. 1935. Bernstein--Lepidopteren. *Deut. Entomol. Z.*, 49: 162-186.

Redell, J.R. 1983. A checklist and bibliography of the Japygoidea (Insecta: Diplura) of North America, Central America, and the West Indies. *Pearce-Sellards Mem. Mus. Ser.*, 37: 1-41.

Rees, B.E. and Ferris, G.F. 1939. The morphology of *Tipula reesi* Alexander (Diptera: Tipulidae). *Microentomology*, 4: 143-178.

Rehn, J.A.G. 1948. The locust genus *Tanaocerus* as found in the United States, and the description of a related new genus (Orthoptera: Acridoidea). *Proc. Acad. Nat. Sci. Philadelphia*, 100: 1-22.

Rehn, J.A.G. and Rehn, J.W.H. 1936. A study of the genus *Hemimerus* (Dermaptera, Hemimerina, Hemimeridae). *Proc. Acad. Nat. Sci.*, 87: 457-508.

Reiss, H. 1936. Ein Zygaenenfund aus der Tertiärzeit. *Entomol. Rund.*, 53: 554-556.

Remm, K.Y. 1976. Late Cretaceous biting midges (Diptera, Ceratopogonidae) from fossil resins of the Khatanga Depression. *Paleontol. J.*, 1976(3): 344-351.

Rempel, J.G. 1975. The evolution of the insect head: the endless dispute. *Quaest. Entomol.*, 11: 9-25.

Rempel, J.G. and Church, N.S. 1971. The embryology of *Lytta viridana* Le Conte (Coleoptera: Meloidae). VII. Eighty-eight to 132 h: the appendages, the cephalic apodemes, and head segmentation. *Can. J. Zool.*, 49: 1571-1581.

Rentz, D.C.F. 1980. A new family of ensiferous Orthoptera from the coastal sands of southeast Queensland. *Mem. Queensland Mus.*, 20: 49-63.

Rentz, D.C.F. 1987. Considerations in naming a family: the Orthoptera and the family Cooloolidae. IN: Baccetti, B.M., (Ed.), *Evolutionary Biology of Orthopteroid Insects*, pp. 433-437. Chichester, U.K.: Ellis Horwood Limited.

Resh, V.H. and Solem, J.O. 1984. Phylogenetic relationships and evolutionary adaptations of aquatic insects. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 66-75. Dubuque: Kendall/Hunt Publishing Co.

Reyne, A. 1927. Untersuchungen uber die mundteile der Thysanopteren. *Zool. Jb.*, **49**: 391-500.

Rice, H.M.A. 1968. An antlion (Neuroptera) and a stonefly (Plecoptera) of Cretaceous age from Labrador, Newfoundland. *Pap. Geol. Surv. Canada*, **68-65**: 1-11.

Richard, C. 1971. Contribution a l'étude morphologique et biologique des Stictococcinae (Hom. Coccoidea). *Ann. Soc. Entomol. France*, N.S., **7**: 571-609.

Richard, G. 1951. L'innervation et les organes sensoriels des pièces buccales du termite a cou jaune (*Calotermes flavicollis* Fab.). *Ann. Sci. Nat. Zool.*, (11), **13**: 397-412.

Richards, A.G. 1973. Anatomy and morphology. IN: Smith, R.F., Mittler, T.E. and Smith, C.N., (Eds.), *History of Entomology*, pp. 185-202. Palo Alto, CA: Annual Reviews, Inc.

Richards, O.W. 1939. The British Bethylidae (s.l.) (Hymenoptera). *Trans. Roy. Entomol. Soc. London*, **89**: 185-344.

Richards, O.W. 1962. *A Revisional Study of the Masarid Wasps (Hymenoptera, Vespoidea)*. London: British Museum (Natural History). 294 p.

Richards, O.W. and Davies, R.G. 1977. *Imms' General Textbook of Entomology*, 10th edn. (2 vols.). London: Chapman and Hall. 1354 p.

Richardson, E.S., Jr. 1956. Pennsylvanian invertebrates of the Mazon Creek area, Illinois: insects. *Fieldiana Geol.* Geol., **12**: 13-56.

Rico-Gray, V., Barber, J.T., Thien, L.B., Ellgaard, E.G. and Toney, J.J. 1989. An unusual animal-plant interaction: feeding of *Schomburgia tibicinis* (Orchidaceae) by ants. *Am. J. Bot.*, **76**: 603-608.

Rieger, C. 1976. Skelett und Muskulatur des Kopfes und Prothorax von *Ochterus marginatus* Latreille. *Zoomorphologie*, **83**: 109-191.

Riek, E.F. 1950. A fossil mecopteron from the Triassic beds at Brookvale, N.S.W. *Rec. Aust. Mus.*, **22**: 254-256.

Riek, E.F. 1953a. Fossil mecopteroid insects from the Upper Permian of New South Wales. *Rec. Aust. Mus.*, **23**: 55-87, pls. 5-6.

Riek, E.F. 1953b. Further Triassic insects from Brookvale, N.S.W. (Orders Orthoptera Saltatoria, Protorthoptera, Perlaria). *Rec. Aust. Mus.*, 23: 161-168.

Riek, E.F. 1954. A re-examination of the Upper Tertiary mayflies described by Etheridge and Olliff from the Vegetable Creek tin-field. *Rec. Aust. Mus.*, 23: 159-160, pl. 11.

Riek, E.F. 1955. Fossil insects from the Triassic beds at Mt. Crosby, Queensland. *Aust. J. Zool.*, 3: 654-691, pls. 1-4.

Riek, E.F. 1956. A re-examination of the mecopteroid and orthopteroid fossils (Insecta) from the Triassic beds at Denmark Hill, Queensland, with descriptions of further specimens. *Aust. J. Zool.*, 4: 98-110, pls. 1-2.

Riek, E.F. 1968a. A new genus and key to the species of Australian Stilbopterygidae (Neuroptera). *J. Aust. Entomol. Soc.*, 7: 105-108.

Riek, E.F. 1968b. A new family of caddis-flies from Australia (Trichoptera: Tasimiidae). *J. Aust. Entomol. Soc.*, 7: 109-114.

Riek, E.F. 1968c. Undescribed fossil insects from the Upper Permian of Belmont, New South Wales. *Rec. Aust. Mus.*, 27: 303-310, pl. 45.

Riek, E.F. 1970a. Lower Cretaceous fleas. *Nature*, 227: 746-747.

Riek, E.F. 1970b. Fossil history. IN: *The Insects of Australia*, 1: 168-186. Commonwealth Scientific and Industrial Research Organization. Melbourne University Press.

Riek, E.F. 1973. Fossil insects from the Upper Permian of Natal, South Africa. *Ann. Natal. Mus.*, 21: 513-532.

Riek, E.F. 1974. Upper Triassic insects from the Molteno "Formation" of South Africa. *Palaeontol. Afr.*, 17: 19-31.

Riek, E.F. 1976a. An entomobryid collembolan (Hexapoda: Collembola) from the Lower Permian of southern Africa. *Palaeontol. Afr.*, 19: 141-143.

Riek, E.F. 1976b. A new collection of insects from the Upper Triassic of South Africa. *Ann. Natal Mus.*, 22: 791-820.

Rietschel, P. 1953. Der Hypopharynx von *Gryllus* und anderen Gryllinae, ein dem Fliegenrussel Analoges Organ. *Z. Morphol. Okol. Tiere*, 41: 386-410.

Riha, P. and Kukalová, J. 1967. Eine neue Tertiare wasserwanze aus dem Bechlejovicer Diatomit (Heteroptera, Belostomatidae). *Acta Entomol. Bohem.*, 64: 259-260, 1 pl.

Riley, C.F.C. 1918. Food of aquatic Hemiptera. *Science*, 48: 545-547.

Riley, C.F.C. 1919. Some habitat responses of the large water strider, *Gerris remiges* Say. *Am. Nat.*, 53: 394-414, 483-505.

Ripley, L.B. 1923. The external morphology and postembryology of noctuid larvae. *Illinois Biol. Mon.*, 8(4): 1-102, pls. 1-7.

Risebrow, A. and Dixon, A.F.G. 1987. Nutritional ecology of phloem-feeding insects. IN: Slansky, F., Jr. and Rodriguez, J.G., *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 421-448. New York: John Wiley and Sons.

Risler, H. 1951. Der Kopf von *Bovicola caprae* (Grult) (Mallophaga). *Zool. Jb. (Anat.)*, 71: 325-374.

Risler, H. 1957. Der Kopf von *Thrips physapus* L. (Thysanoptera, Terebrantia). *Zool. Jb. (Anat.)*, 76: 251-302.

Rivnay, E. 1929. Revision of the Rhipiphoridae of North and Central America (Coleoptera). *Mem. Am. Entomol. Soc.*, 6: 1-68, pls. 1-4.

Rober, H. 1941. Morphologie des Kopfes und des Vorderdarmes der Larve und Imago von *Sialis flavilatera*. *Zool. Jb. (Anat.)*, 67: 61-118.

Roberti, D. 1977. Descrizione dello *Scymnus* (*Nephus*) *kiesenwetteri* Muls. (Coleoptera-Coccinellidae). *Entomologica*, 13: 21-30.

Roberts, M.J. 1969. Structure of the mouthparts of the larvae of the flies *Rhagio* and *Sargus* in relation to feeding habits. *J. Zool.*, 159: 381-398.

Roberts, M.J. 1970. The structure of the mouthparts of syrphid larvae (Diptera) in relation to feeding habits. *Acta Zool.*, 51: 43-65.

Roberts, M.J. 1971. The structure of the mouthparts of some calypterate dipteran larvae in relation to their feeding habits. *Acta Zool.*, 12: 171-188.

Roberts, M.J. 1972. The structure and function of the maxillary appendages in the American cockroach, *Periplaneta americana* (L.). *Forma Funct.*, 5: 253-272.

Robinson, G.G. 1939. The mouthparts and their function in the female mosquito, *Anopheles maculipennis*. *Parasitology*, 31: 212-242.

Robinson, H. and Vockeroth, J.R. 1981. Dolichopodidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol.1. *Res. Branch Agr. Canada*, **27**: 625-640.

Robinson, I. 1953. The postembryonic stages in the life cycle of *Aulacigaster leucopeza* (Meigen) (Diptera Cyclorrhapha: Aulacigasteridae). *Proc. Roy. Entomol. Soc. London*, **28A**: 77-84.

Robinson, V.E. 1930. The mouth-parts of the larval and adult stages of *Dermestes vulpinus* F. *Ann. Entomol. Soc. Am.*, **23**: 399-416.

Roer, H. 1975. Zur Lebensweise des Namibwüstenkäfers *Onymacris plana*. *Bonn. Zool. Beit.*, **26**: 239-256.

Rogers, J.S. 1926. Some notes on the feeding habits of adult crane-flies. *Florida Entomol.*, **10**: 33-38.

Rogers, J.S. 1927. Notes on the biology and immature stages of *Geranomyia* (Tipulidae, Diptera). I. *Geranomyia rostrata* (Say). *Florida Entomol.*, **11**: 17-26.

Rogers, J.S. 1932. On the biology of *Limonia* (*Dicranomyia floridana*) (Osten Sachen). *Florida Entomol.*, **15**: 65-70.

Rogers, J.S. 1933. The ecological distribution of the crane-flies of northern Florida. *Ecol. Mon.*, **3**: 1-74.

Rohdendorf, B.B. 1938. Dipterous insecta of the Mesozoic of Karatau. I. Brachycera and part of the Nematocera. *Trans. Paleontol. Inst.*, **7**: 29-67.

Rohdendorf, B.B. 1946. The evolution of the wing and the phylogeny of Oligoneura (Diptera, Nematocera). *Trans. Paleontol. Inst.*, **13**: 1-108, pls. 1-16.

Rohdendorf, B.B. 1957. Palaeoentomological investigations in the USSR. *Trans. Paleontol. Inst.*, **66**: 1-102. [In Russian.]

Rohdendorf, B.B. 1961. Superorder Coleopteroidea. IN: Rohdendorf, B.B., Bekker-Migdisova, E.E., Martynova, O.M. and Sharov, A.G., "Paleozoic Insects of the Kusnetsk Basin." *Trans. Paleontol. Inst.*, **85**: 393-469. [In Russian.]

Rohdendorf, B.B. 1962. Order Diptera. IN: *Principles of Paleontology*, pp. 50-72. Moscow: Academy of Sciences. [In Russian.]

Rohdendorf, B.B. 1968a. *Jurassic Insects of Karatau*. Moscow: Academy of Sciences. 252 p., 25 pls. [In Russian.]

Rohdendorf, B.B. 1968b. New Mesozoic nemestrinids (Diptera, Nemestrinidae). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 180-189. Moscow: Academy of Sciences. [In Russian.]

Rohdendorf, B.B. 1974. *Historical Development of the Diptera*. [Translated from the Russian by J.E. Moore and I. Thiele.] Edmonton: University of Alberta Press. 360 p.

Rohdendorf, B.B. 1980. Order Muscida. IN: Rohdendorf, B.B. and Rasnitsyn, A.G., (Eds.), "Historical Development of the Class Insecta." *Trans. Paleontol. Inst.*, **175**: 112-122. [In Russian.]

Rohdendorf, B.B., Bekker-Migdisova, E.E., Martynova, O.M. and Sharov, A.G. 1961. Paleozoic insects from the Kusnetsk Basin. *Trans. Paleontol. Inst.*, **85**: 1-705, pls. 1-40. [In Russian.]

Rohdendorf, B.B. and Kalugina, N.S. 1974. The discovery of a member of the peculiar family Nymphomyiidae (Diptera) in the maritime territory. *Entomol. Rev.*, **53**: 146-151.

Rohdendorf, B.B. and Rasnitsyn, A.P. 1980. Historical development of the Class Insecta. *Trans. Paleontol. Inst.*, **175**: 1-269, pls. 1-8. [In Russian.]

Rohwer, S.A. 1917. *Idiogastra*, a new suborder of Hymenoptera with notes on the immature stages of *Oryssus*. *Proc. Entomol. Soc. Washington*, **19**: 89-99.

Rolfe, W.D.I. 1980. Early invertebrate terrestrial faunas. IN: Panchen, A.L., (Ed.), "The Terrestrial Environment and the Origin of Land Vertebrates." *Syst. Assn. Spec. Publ.*, **15**: 117-157.

Romoser, W.S. 1973. *The Science of Entomology*. New York: Macmillan Publ. Co. 449 p.

Roonwal, M.L. and Sangal, S.K. 1960. Variability in the mandibles of soldiers in the termite *Odontotermes obesus* (Rambur) (Isoptera, Family Termitidae). *Rec. Indian Mus.*, **55**: 1-22.

Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Mon.*, **37**: 317-350.

Roskam, J.C. 1982. Larval characters of some eurytomid species (Hymenoptera, Chalcidoidea). *Proc. Konikl. Ned. Akad. Wetensch.*, **85**: 293-305.

Ross, D.H. and Craig, D.A. 1980. Mechanisms of fine particle capture by larval black flies (Diptera: Simuliidae). *Can. J. Zool.*, **58**: 1186-1192.

Ross, E.S. 1952. The identity of *Teratembia geniculata* Krauss and a new status for the family Teratembiidae (Embioptera). *Wassman J. Biol.*, 10: 225-234.

Ross, E.S. 1982. Embiidina. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 387-389. New York: McGraw-Hill Book Co.

Ross, H.H. 1958. The Cretaceous caddisfly, *Dolophilus praemissus* Cockerell. *Trans. Tenth Int. Congr. Entomol.*, 1: 849.

Ross, H.H. 1967. The evolution and past dispersal of the Trichoptera. *Ann. Rev. Entomol.*, 12: 169-206.

Ross, H.H., Ross, C.A. and Ross, J.R.P. 1982. *A Textbook of Entomology*. New York: John Wiley. 696 p.

Roth, L.M. 1982. Blattaria. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 346-347. New York: McGraw-Hill Book Co.

Rothschild, N.C. 1906. The physiological anatomy of the mouth-parts and alimentary canal of the Indian rat flea, *Pulex cheopis*, Rothschild. *J. Hyg.*, 6: 486-495.

Rothwell, G.W. and Scott, A.C. 1983. Coprolites within marittiaceous fern stems (*Psaronius magnificus*) from the Upper Pennsylvanian of the Appalachian Basin, U.S.A. *Palaeogeog., Palaeoclim., Palaeoecol.*, 41: 227-232.

Rothwell, G.W. and Scott, A.C. 1988. *Heterotheca* Benson; lyginopterid pollen organs or coprolites? *Bull. Brit. Mus. Nat Hist., (Geol.)*, 44: 41-43.

Rouchy, R. 1964. Squelette et musculature cephaliques de deux types d'imagos de lepidopteres heteroneures. *Trav. Lab. Zool., Univ. Dijon*, 61: 1-59.

Rousset, A. 1936. Sur l'anatomie cephalique les larves Coniopterygidae (Neuropteres Planipennes). *C.R. Acad. Sci., Paris*, 242: 934-936.

Rousset, A. 1966. Morphologie cephalique des larves de Planipennes (Insectes Nevropteroides). *Mem. Mus. Natl. Hist. Nat.*, 42: 1-199.

Rowell, H.F. 1978. Food plant specificity in neotropical rain-forest acridids. *Entomol. Exp. Appl.*, 24: 451-462.

Rozefelds, A.C. 1985. The first records of fossil leaf mining from Australia. IN: Cooper, R., (Ed.), *Hornibrook Symp., Extend. Abstr.*, pp. 80-81. Christchurch: Department of Scientific and Industrial Research.

Rozefelds, A.C. and Sobbe, I. 1987. Problematic insect leaf mines from the Upper Triassic Ipswich Coal Measures of southeastern Queensland, Australia. *Alcheringa*, **11**: 51-57.

Rozen, J.G., Jr. 1958. The external anatomy of the larva of *Nacerdes melanura* (Linneaus) (Coleoptera: Oedemeridae). *Ann. Entomol. Soc. Am.*, **51**: 222-229.

Rozen, J.G., Jr. 1964. Phylogenetic-taxonomic significance of last instar of *Protoxaea gloriosa* Fox, with descriptions of first and last instars (Hymenoptera: Apoidea). *Proc. New York Entomol. Soc.*, **72**: 223-230.

Rozen, J.G., Jr. 1970. Biology, immature stages, and phylogenetic relationships of fideliine bees, with the description of a new species of *Neofidelia* (Hymenoptera, Apoidea). *Am. Mus. Novit.*, **2427**: 1-25.

Rubenstein, D.I. and Koehl, M.A.R. 1977. The mechanisms of filter feeding. Some theoretical considerations. *Am. Nat.*, **111**: 981-994.

Rudolph, R. 1970. Studies on the ecology, ethology and functional morphology of *Nebria complanata* L. (Coleoptera, Carabidae). *Forma Funct.*, **2**: 189-237.

Russell, L.M. 1941. A classification of the scale insect genus *Asterolecanium*. *U.S. Dept. Agr. Misc. Publ.*, **424**: 1-322.

Rymer-Roberts, A.W. 1921. On the life history of "wireworms" of the genus *Agriotes*, Esch., with some notes on that of *Athous haemorrhoidalis*, F. *Ann. Appl. Biol.*, **8**: 193-215, pl. 4.

Rymer-Roberts, A.W. 1958. On the taxonomy of Erotylidae (Coleoptera) with special reference to the morphological characters of the larvae. II. *Trans. Roy. Entomol. Soc. London*, **110**: 245-285.

Sabrosky, C.W. 1963. A new acalyptrate fly from the Tertiary amber of Mexico. *J. Paleontol.*, **37**: 119-120, pl. 16.

Sabrosky, C.W. 1981. Asteiidae. IN: McAlpine, J.F., et. al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, **28**: 899-902.

Salem, H.H. 1931. Some observations on the structure of the mouthparts of the fourth stage larva of *Aedes* (*Stegomyia*) *fasciata* (Fab.). *Ann. Trop. Med. Parasitol.*, 25: 393-419.

Salmon, J.T. 1964. An index to the Collembola. *Bull. Roy. Soc. New Zealand*, 7: 1-651.

Salt, G. 1931. Three bees from Baltic amber. *Bernstein-forschungen*, 2: 136-147.

Sanborne, M. 1981. Biology of *Ithycerus noveboracensis* (Forster) (Coleoptera) and weevil phylogeny. *Evol. Mon.*, 4: 1-80.

Sanderson, M.W. and Farr, T.H. 1960. Amber with insect and plant inclusions from the Dominican Republic. *Science*, 131: 1313.

Sanz, J.L., Wenz, S., Yebenes, A., Estes, R., Martinez-Gelclos, X., Jimenez-Fuentes, E., Diéguez, C., Buscalioni, A.D., Barbadillo, L.J. and Via, L. 1988. An Early Cretaceous faunal and floral continental assemblage: Las Hoyas fossil site (Cuenca, Spain). *Geobios*, 21: 611-635.

Satija, R.C. and Satija, G.R. 1959. Food in relation to mouth-parts and alimentary canal of *Wormaldia occipitalis* Pictet (Philopotamidae) larvae. *Res. Bull. Punjab Univ.*, 10: 169-178.

Sattler, W. 1958. Beitrage zur Kenntnis von Lebensweise und Korperbau der Larve und Puppe von *Hydropsyche* Pict. (Trichoptera), mit besonderer berucksichtigung des Netzbaues. *Z. Morphol. Okol. Tiere*, 47: 115-192.

Saunders, E. 1891. On the tongues of the British Hymenoptera Anthophila. *J. Linn. Soc.*, 23: 410-432.

Saunders, L.G. 1923. On the larva, pupa, and systematic position of *Orphnephila testacea*, Macq. (Diptera Nematocera). *Ann. Mag. Nat. Hist.*, (9), 11: 631-640, pls. 7-8.

Saunders, W.B., Mapes, R.H., Carpenter, F.M. and Elsik, W.C. 1974. Fossiliferous amber from the Eocene (Claiborne) of the Gulf Coastal Plain. *Geol. Soc. Am. Bull.*, 85: 979-984.

Savigny, M.-J.C., 1816. Mémoires sur les Animaux sans Vertébres.

Saxena, K.N. 1963. Mode of ingestion of a heteropterous insect *Dysdercus koenigii* (F.) (Pyrrhocoridae). *J. Insect Physiol.*, 9: 47-71.

Scarbrough, A.G. 1978. Ethology of *Cerotainia albipilosa* Curran (Diptera: Asilidae) in Maryland: courtship, mating and oviposition. *Proc. Entomol. Soc. Washington*, 80: 179-190.

Scegoleva-Barovskaya, T. 1929. Der erste Vertreter der Familie Mordellidae aus der Juraformation Turkestans. *Dokl. Acad. Sci. USSR*, **1929**: 27-29.

Schaeffer, C.W. 1979. Feeding habits and hosts of calypterate flies (Diptera: Brachycera, Cyclorrhapha). *Entomol. Gen.*, **5**: 193-200.

Schaller, F. 1970. Collembola (Springschwänze). IN: Beier, M., (Ed.), *Handbuch der Zoologie*, Band 4, Hälfte 2, Lfg. **12**: 1-72.

Schaller, F. and Wolter, H. 1963. Bau und Funktion der stechend-saugenden Mundwerkzeuge der Collembolen. *Deut. Zool. Gesselsch. Verhandl.*, **1963**: 440-447.

Schedl, K.E. 1962. New Platypodidae from Mexican amber. *J. Paleontol.*, **36**: 1035-1038.

Schicha, E. 1967. Morphologie und Funktion der Malachiiden-mundwerkzeuge unter besonderer Berucksichtigung von *Malachius bipustulatus* L. (Coleopt., Malacodermata. *Z. Morphol. Okol. Tiere*, **60**: 376-433.

Schiemenz, H. 1957. Vergleichende funktionell-anatomische Untersuchungen der Kopfmuskulatur von *Theobaldia* und *Eristalis* (Dipt. Culicid. und Syrphid.). *Deut. Entomol. Z.*, N.S., **4**: 268-331.

Schimmer, F. 1909. Beitrag zu einer Monographie der Gryllodeen-gattung *Myrmecophila* Latr. *Z. Wiss. Zool.*, **93**: 409-534.

Schiodte, J.C. 1865. On the classification of *Cerambyces*, with particular regard to the Danish fauna. *Ann. Mag. Nat. Hist.*, (3), **15**: 182-209.

Schlee, D. 1969. Verwandtschaftsbeziehungen innerhalb der Sternorrhyncha aufgrund synapomorpher Merkmale. Phylogenetische Studien an Hemiptera II. Aphidiformes (Aphidina + Coccina) als monophyletische Gruppe. *Stutt. Beitr. Naturk.*, **199**: 1-72.

Schlee, D. 1970. Insektenfossilien aus der unteren Kreide. I. Verwandtschaftsforschung an fossilen und rezenten Aleyrodina (Insecta, Hemiptera). *Stutt. Beitr. Naturk.*, **213**: 1-72.

Schlee, D. 1972. Bernstein aus dem Libanon. *Kosmos*, **1972**: 460-463.

Schlee, D. and Dietrich, H.-G. 1970. Insektenführender Bernstein aus der Unterkreide des Libanon. *Neues Jb. Geol. Paläont. Monat.*, **1**: 40-50.

Schlee, D. and Glockner, W. 1978. Bernstein. Bernsteine und Bernsteine-Fossilen. *Stutt. Beitr. Naturk.*, (C), **8**: 1-72.

Schlein, Y. 1980. Morphological similarities between the skeletal structures of Siphonaptera and Mecoptera. IN: Traub, R. and Starcke, H., (Eds.), *Fleas*, pp. 359-367. Rotterdam: A.A. Balkema.

Schlinger, E.I. 1981. Acroceridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 575-584.

Schlüter, T. 1974. Kritisches zum Nachweis von Schmetterlings schuppen aus einem fossilen Harz der mittlern Kreide Nordwest-frankreichs. *Entomol. Z.*, 84: 253-256.

Schlüter, T. 1975. Nachweis verschiedener Insecta-Ordines in einem mittelkretazischen Harz Nordwestfrankreichs. *Entomol. Germ.*, 1: 151-161.

Schlüter, T. 1976. Die Wollschweber-Gattung *Glabellula* (Diptera: Bombyliidae) aus dem oligozanen Harz der Dominikanischen Republik. *Entomol. Germ.*, 2: 355-363.

Schlüter, T. 1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphrozönose uas dem Cenomanium von NW Frankreich. *Berl. Geowiss. Abh.*, (A), 9: 1-150, pls. 1-9.

Schmalfuss, H. 1979. *Proceroplatus henningi* n.sp., die erste Plizmücke aus dem Dominikanischen Bernstein (Stuttgarter Bernstein-sammlung: Diptera, Mycetophiloidea, Keroplatidae). *Stutt. Beitr. Naturk.*, (B), 49: 1-9.

Schmid, R., 1988. Morphologische Anpassungen in einem Räuber-Beute-System: Ameisenkäfer (Scydmaenidae, Staphylinoidea) und gepanzerte Milben (Acari). *Zool. Jb. (Syst.)*, 115: 207-228.

Schmidtgen, O. 1938. Die Fundstelle von Pflanzen und Insekten in den Hydrobienkalken am Petersberg bei Mainz-Kastel. *Paläont. Z.*, 20: 1-9, pls. 1-2.

Schmitt, J.B. 1938. The feeding mechanism of adult Lepidoptera. *Smithson. Misc. Collns.*, 97: 1-28.

Schmitz, G. 1943. Le labium et les structures buccopharyngiennes du genre *Stenus* Latreille. *Cellule*, 49: 291-334.

Schneider, D. 1964. Insect antennae. *Ann. Rev. Entomol.*, 9: 103-122.

Scholl, G. 1969. Die Embryonalentwicklung des Kopfes und Prothorax von *Carausius morosus* Br. (Insecta, Phasmida). *Z. Morphol. Okol. Tiere*, 65: 1-142.

Schonmann, H. 1981. Zur Kopfmorphologie der Ephemeriden-larven *Siphlonurus aestivalis* Eaton und *Lepeorus goyi goyi* Peters. *Zoologica*, **45**: 1-51.

Schowalter, T.D., Stafford, S.G. and Slagle, R.L. 1988. Arboreal arthropod community structure in an early successional coniferous forest ecosystem in western Oregon. *Great Basin Nat.*, **48**: 327-333.

Schram, F.R. 1986. *Crustacea*. Oxford: Oxford University Press. 606 p.

Schremmer, F. 1950a. Morphologische und funktioinelle Analyse der Mundteile und des Pharynx der Larve von *Anopheles maculipennis* Meig. *Oster. Zool. Z.*, **2**: 173-222.

Schremmer, F. 1950b. Bau und Funktion der Larvenmundteile der Dipterengattung *Dixa* Meigen. *Oster. Zool. Z.*, **2**: 379-413.

Schremmer, F. 1952. Die Mundteile der Brachycerenlarven und der Kopfbau der Larve von *Stratiomys chamaeleon* L. *Oster. Zool. Z.*, **3**: 326-397.

Schremmer, F. 1956. Funktionsmorphologische Studien an Dipterenlarven. *Verhandl. Deut. Zool. Ges.*, **1956**: 301-305.

Schuhmacher, H. and Hoffmann, H. 1982. Zur Funktion der Mundwerkzeuge von Schwebfliegen bei der Nahrungsaufnahme (Diptera: Syrphidae). *Entomol. Gen.*, **7**: 327-342.

Schumann, H. 1984. Erstnachweis einer Rabufliege aus dem Sächsischen Bernstein. *Deut. Entomol. Z.*, N.F., **31**: 217-223.

Schumann, H. and Wendt, H. 1989. Zur Kenntnis der tierischen Inklusen des Sächsischen Bernsteins. *Deut. Entomol. Z.*, N.F., **36**: 33-44.

Schutze, K.T. 1931. *Die Biologie der Kleinschmetterling unter besonderer Berücksichtigung ihrer Nährpflanzen und Erscheinungszeiten.* Frankfurt au Maim. 235 pp.

Schwaller, W. 1986. Fossile Käfer aus miozänen Sedimenten des Randecker Maars in Südwest-Deutschland (Insecta, Coleoptera). *Stutt. Beitr. Naturk.*, (B), **126**: 1-9.

Schwartz, N.F. 1948. Stingless bees (Meliponidae) of the Western Hemisphere. *Bull. Am. Mus. Nat. Hist.*, **90**: i-xvii + 1-546.

Scopoli, J.A. 1777. *Introduction ad Historiam Naturalem Sistens Genera Lapidum, Plantarum et Animalium*. Prague: Gerle. 604 pp.

Scott, A.C. and Paterson, S. 1984. Techniques for the study of plant/arthropod interactions in the fossil record. *Geobios Spec. Mem.*, **8**: 449-455, pl. 1.

Scott, A.C. and Taylor, T.N. 1983. Plant/animal interactions during the Upper Carboniferous. *Bot. Rev.*, **49**: 259-307.

Scott, J.A. 1986. *The Butterflies of North America: A Natural History and Field Guide*. Natural History and Field Guide. Stanford, CA: Stanford University Press. 583 p.

Scourfield, D.J. 1940. The oldest known fossil insect (*Rhyniella praecursor* Hirst & Maulik)--further details from additional specimens. *Proc. Linn. Soc. London*, **152**: 113-131.

Scudder, G.G.E. 1962. Results of the Royal Society expedition to southern Chile, 1958-59; Lygaeidae (Hemiptera), with the description of a new subfamily. *Can. Entomol.*, **94**: 1064-1075.

Scudder, S.H. 1885. Notes on Mesozoic cockroaches. *Proc. Acad. Nat. Sci. Philadelphia*, **1885**: 105-115.

Scudder, S.H. 1889. The fossil butterflies of Florissant. *Ann. Rept. U.S. Geol. Surv.*, **8**: 439-474.

Scudder, S.H. 1890. The Tertiary insects of North America (Coccinea). *U.S. Geol. Surv. Territ.*, 13: 241-242.

Scudder, S.H. 1892. Some insects of special interest from Florissant, Colorado and other points in the Tertiaries of Colorado and Utah. *U.S. Geol. Surv. Bull.*, **93**: 1-25, pls. 1-3.

Scudder, S.H. 1893. Tertiary rhynchophorous Coleoptera of the United States. *Mon. U.S.Geol. Surv.*, **21**: 1-206, pls. 1-12.

Scudder, S.H. Adephagous and clavicorn Coleoptera from the Tertiary deposits at Florissant, Colorado with descriptions of a few rhynchophorous Tertiary Coleoptera of North America. *Mon. U.S. Geol. Surv.*, **40**: 1-148, pls. 1-11.

Seamans, H.L. 1920. The external anatomy of *Anthomyia radicum* Linn. (Diptera, Anthomyidae). *Ann. Entomol. Soc. Am.*, **13**: 201-216, pls. 17-22.

Seevers, C.H. and Dybas, H.S. 1943. A synopsis of the Limulodidae (Coleoptera): a new family proposed for myrmecophiles of the subfamilies Limulodinae (Ptiliidae) and Cephaloplectinae (Staphylinidae). *Ann. Entomol. Soc. Am.*, **36**: 546-586.

Sehgal, S.S. 1963. The skeleto-musculature of the common Indian yellow wasp, *Polistes olivaceus* (De Geer). I. The head and its appendages. *Proc. Zool. Soc. India*, **16**: 153-167.

Selden, P.A. 1985. Eurypterid respiration. *Phil. Trans. Roy. Soc. London*, (B), **309**: 219-226.

Selden, P.A. and Edwards, D. 1989. Colonisation of the land. IN: Allen, K.C. and Brigs, D.E.G., (Eds.), *Evolution and the Fossil Record*, pp. 122-152. London: Belhaven Press.

Sellards, E.H. 1907. Types of Permian insects. *Am. J. Sci.*, (4), **23**: 345-355.

Sen Gupta, T. and Crowson, R.A. 1966. A new family of cucujoid beetles, based on six Australian and one New Zealand genera. *Ann. Mag. Nat. Hist.*, (13), **9**: 61-85.

Sen Gupta, T. and Crowson, R.A. 1969a. On a new family of Clavicornia (Coleoptera) and a new genus of Languriidae. *Proc. Roy. Entomol. Soc. London*, (B), **38**: 125-131.

Sen Gupta, T. and Crowson, R.A. 1969b. Further observations on the family Boganiidae, with definition of two new families Cavognathidae and Phloestichtidae. *J. Nat. Hist.*, **3**: 571-590.

Sen Gupta, T. and Crowson, R.A. 1973. A review of the classification of Cerylonidae (Coleoptera, Clavicornia). *Trans. Roy. Entomol. Soc. London*, **124**: 365-446.

Senior-White, R. 1922-23. A note on pseudo-tracheal teeth in the "eye-fly" (*Siphunculina funicola* De Meijere). *Indian J. Med. Res.*, **10**: 825-826, pl. 61.

Sepkoski, J.J. and Hulver, M.L. 1985. An atlas of Phanerozoic clade diversity diagrams. IN: Valentine, J.W., (Ed.), *Phanerozoic Diversity Patterns: Profiles in Macroevolution*, pp. 11-39. Princeton: Princeton University Press.

Servadei, A. 1946. Reperti sulla costituzione dell'apparato boccale delle specie appartenenti alle famiglie Gerridae, Veliidae e Hydrometridae (Hemiptera, Heteroptera). *Boll. Entomol. Bologna*, **15**: 217-228.

Setty, L.R. 1940. Biology and morphology of some North American Bittacidae (Order Mecoptera). *Am. Midl. Nat.*, **23**: 257-353.

Setty, L.R. 1941. Description of the larva of *Bittacus apicalis* and a key to bittacid larvae (Mecoptera). *J. Kansas Entomol. Soc.*, **14**: 64-65.

Shalaby, A.M. 1956. On the mouth parts of the larval instars of *Anopheles quadrimaculatus* (Say) (Diptera: Culicidae-Anophelini). *Bull. Soc. Entomol. Egypte*, **40**: 137-174.

Shalaby, A.M. 1957a. On the mouth parts of the larval instars of *Aedes aegypti* (L.). *Bull. Soc. Entomol. Egypte*, **41**: 145-177.

Shalaby, A.M. 1957b. On the mouth parts of the larval instars of *Culex quinquefasciatus* (Say). *Bull. Soc. Entomol. Egypte*, 41: 269-297.

Shaposhnikov, G.K. 1980. Evolution of morphological structures in aphids (Homoptera, Aphidinea) and the mode of life of Recent and Mesozoic aphids. *Entomol. Rev.*, **59**: 29-48.

Shaposhnikov, G.C. 1985. The main features of the evolution of aphids. *Proc. Int. Aphidological Symp.*, pp. 19-99. Warsaw: Institute of Zoology, Polish Academy of Sciences.

Shaposhnikov, G.C. 1987. Evolution of aphids in relation to evolution of plants. IN: Minks, A.K. and Harrewijn, P., (Eds.), *Aphids: Their Biology, Natural Enemies and Control*, **A**: 409-414. Amsterdam: Elsevier.

Sharif, M. 1937. On the internal anatomy of the larva of the rat-flea, *Nosopsyllus fasciatus* (Bosc). *Phil. Trans. Roy. Soc. London*, (B), **227**: 465-538.

Sharov, A.G. 1948. Triassic Thysanura from the Ural foreland. *Dokl. Akad. Nauk USSR*, N.S., **61**: 517-519. [In Russian.]

Sharov, A.G. 1953. The first discovery of a Permian larva of Megaloptera from Kargala. *Dokl. Akad. Nauk SSSR*, **1953**(4): 731-732. [In Russian.]

Sharov, A.G. 1957a. The first record of Cretaceous Aculeata. *Dokl. Akad. Nauk USSR*, **112**: 943-954. [In Russian.]

Sharov, A.G. 1957b. The distinctive Paleozoic wingless insects of the new order Monura (Insecta, Apterygota). *Dokl. Akad. Nauk SSSR*, **115**: 795-798. [In Russian.]

Sharov, A.G. 1961. Order Plecoptera. IN: Rohdendorf, B.B., Bekker-Migdisova, E.E., Martynova, O.M. and Sharov, A.G., Paleozoic insects of the Kuznetsk Basin. *Trans. Paleontol. Inst.*, **85**: 225-234. [In Russian.]

Sharov, A.G. 1962. A new Permian family of grasshoppers (Orthoptera). *Paleontol. Zhur.*, **2**: 112-116 [In Russian.]

Sharov, A.G. 1966. *Basic Arthropodan Stock with Special Reference to Insects*. Oxford: Pergamon Press. 171 p.

Sharov, A.G. 1971. Phylogeny of the Orthopteroidea. *Trans. Inst. Paleontol*, **118**: 1-251. [Translated version.]

Sharov, A.G. 1973. The phylogenetic relations of the Order Thysanoptera. *Entomol. Rev.*, **51**: 506-508.

Sharp, D. 1922. Insects. Part I. Introduction, Aptera, Orthoptera, Neuroptera, and a portion of Hymenoptera (Sessiliventres and Parasitica). IN: Harmer, S.F. and Shiple, A.E., (Eds.), *The Cambridge Natural History*, 5: 81-565.

Shear, W.A. 1990. [Devonian arthropod faunas.] *Short Course Paleontol.*, 3, in press.

Shear, W.A., Bonamo, P.M., Grierson, J.D., Rolfe, W.D.I., Smith, E.L. and Norton, R.A. 1984. Early land animals in North America: evidence from Devonian age arthropods from Gilboa, New York. *Science*, **224**: 492-494.

Shear, W.A., Selden, P.A., Rolfe, W.D.I., Bonamo, P.M. and Grierson, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). *Am. Mus. Novit.*, **2901**: 1-74.

Shellford, R. 1910. On a collection of Blattidae preserved in amber, from Prussia. *J. Linn. Soc. London*, **30**: 336-355.

Shewell, G.E. 1960. Notes on the family Odiniidae with a key to the genera and descriptions of new species (Diptera). *Can. Entomol.*, **92**: 625-633.

Shewell, G.E. 1987. Sarcophagidae. IN: McAlpine, J.F. et al., (Eds.), "Manual of Nearctic Diptera,", vol. 2. *Res. Branch Agr. Canada*, **28**: 1159-1186.

Shields, O. 1976. Fossil butterflies and the evolution of Lepidoptera. *J. Res. Lepidoptera*, **15**: 132-143.

Shields, O. 1988. Mesozoic history and neontology of Lepidoptera in relation to Trichoptera, Mecoptera, and angiosperms. *J. Paleontol.*, **62**: 251-258.

Shortt, H.E. and Swaminath, C.S. 1928. The method of feeding of *Phlebotomus argentipes* with relation to its bearing on the transmission of kala-azar. *Indian J. Med. Res.*, **15**: 827-836.

Short, J.R.T. 1951. Some aspects of the morphology of the insect head as seen in the Lepidoptera. *Proc. Roy. Entomol. Soc. London*, (A), **26**: 77-88.

Short, J.R.T. 1952. The morphology of the head of larval Hymenoptera with special reference to the head of the Ichneumonoidea, including a classification of the final instar larvae of the Braconidae. *Trans. Roy. Entomol. Soc. London*, **103**: 27-66.

Short, J.R.T. 1954. A grouping by larval characters of some species of the genus *Apanteles* (Hymenoptera: Braconidae). *Bull. Entomol. Res.*, **44**: 327-332.

Short, J.R.T. 1955. The morphology of the head of *Aeshna cyanea* (Muller) (Odonata: Anisoptera). *Trans. Roy. Entomol. Soc. London*, **106**: 197-211.

Siewing, R. 1962. Zum Problem der Arthropodenkopfsegmentierung. *Zool. Anz.*, **169**: 429-468.

Sikes, E.K. 1930. Larvae of *Ceratophyllus wickhami* and other species of fleas. *Parasitology*, **12**: 242-259.

Sih, A. 1987. Nutritional ecology of aquatic insect predators. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 579-607. New York: John Wiley and Sons.

Silvestri, F. 1905. Descrizione di un nuovo genere di Rhipiphoridae. *Redia*, **3**: 315-324.

Silvestri, F. 1907. Decrizione di novo genera d'insetti Apterigoti representante di un novo ordine. *Bull. Lab. Zool., Portici*, **1**: 296-311.

Silvestri, F. 1912. Die Thysanuren des baltischen Bernsteins. *Schrift. Physik.-Okon. Ges. Köningsberg*, **53**: 42-66.

Silvestri, F. 1924. Contribuzioni alla conoscenza Tortricidi delle querce. *Boll. Lab. Zool. Gen. Agr. Portici*, **27**: 41-107.

Silvestri, F. 1933. Sulle appendici del capo degli "Japygidae" (Thysanura Entotropha) e rispettivo confronto con quelle dei chilopodi, dei diplopodi e dei crostacei. *Proc. Fifth Int. Congr. Entomol.*, **2**: 329-343.

Singh, S. 1971. Morphology of the head of Homoptera. *Res. Bull. Punjab. Univ.*, **22**: 261-316.

Sinha, R.N. 1968. Adaptive significance of mycophagy in stored-product Arthropoda. *Evolution*, **22**: 785-798.

Sinichenkova, N.D. 1975. Mayfly larvae of the family Hexagenitidae (Insecta, Ephemeroptera). *Paleontol. J.*, **1975**(1): 80-85.

Sinichenkova, N.D. 1976. New Early Cretaceous mayflies (Insecta, Ephemeroptera) from eastern Transbaikalia. *Paleontol. J.*, **1976**(2): 189-197.

Sinichenkova, N.D. 1983. New Jurassic stoneflies (Perlida) from Transbaikalia. *Paleontol. J.*, **1983**(1): 94-101.

Sinichenkova, N.D. 1985. New Jurassic stone flies of the Family Baleyopterygidae. *Paleontol. J.*, **19**: 129-134.

Sinichenkova, N.D. 1987. The historical development of the Plecoptera. *Trans. Paleontol. Inst.*, **221**: 1-142.

Sinton, J.A. and Covell, G. 1927. The relation of the morphology of the buccal cavity to the classification of anopheline mosquitoes. *Indian J. Med. Res.*, **15**: 301-309, pls. 29-33.

Skalski, A.W. 1973a. Studies on the Lepidoptera from fossil resins. Part II. *Epiborkhausenites obscurotrimaculatus* gen. et sp. nov. (Oecophoridae) and a tineid-moth discovered in the Baltic amber. *Acta Palaeontol. Pol.*, **28**: 153-160.

Skalski, A.W. 1973b. Studies on the Lepidoptera from fossil resins. Part VI. *Tortricidrosis inclusa* gen. et spec. nov. from the Baltic amber (Lep., Tortricidae). *Deut. Entomol. Z.*, N.F., **20**: 339-344.

Skalski, A.W. 1974. Zwei neue Gattungen und Arten der Familie Tineidae aus dem baltischen Bernstein. Studien an Lepidopteren aus fossilen Harzen--V. *Beit. Entomol.*, **24**: 97-104.

Skalski, A.W. 1976a. Les lèpidoptères fossiles de l'ambre: etat actuel de nos connaissances. *Linn. Belg.*, **6**: 154-169.

Skalski, A.W. 1976b. Les lèpidoptères fossiles de l'amber: etat actual de nos connaissances (2e partie). *Linn. Belg.*, **6**: 195-208.

Skalski, A.W. 1976c. Les lèpidoptères fossiles de l'amber. Etat actuel de nos connaissances (3e partie et fin). *Linn. Belg.*, **6**: 221-233.

Skalski, A.W. 1979a. A new member of the Family Micropterygidae (Lepidoptera) from the Lower Cretaceous of Transbaikalia. *Paleontol. J.*, **1979**(3): 206-214.

Skalski, A.W. 1979b. Records of oldest Lepidoptera. *Nota Lepid.*, 2: 61-66.

Skalski, A.W. 1984a. Mesozoic Lepidoptera with emphasis to early evolution of the order. *Abstr. 17th Int. Congr. Entomol.*, p. 8.

Skalski, A.W. 1984b. A new Lower Cretaceous Lepidoptera (Homoneura). *Bull. Polish Acad. Sci., Biol. Ser.*, 32: 389-394.

Skoblo, V.M. 1966. New data on the biostratigraphy of the Udinskaya Formation. *Mater. Geol. Min. Resour. Buryat ASSR*, 10: 66-75. [In Russian.]

Slack, H.D. 1936. The food of caddis fly (Trichoptera) larvae. *J. Anim. Ecol.*, 5: 105-115.

Slansky, F., Jr. and Panizzi, A.R. 1987. Nutritional ecology of seed-sucking insects. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 283-320. New York: John Wiley and Sons.

Slansky, F., Jr. and Rodriguez, J.G., (Eds.). 1987. *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates.* New York: John Wiley and Sons. 1016 pp.

Slater, J.A. 1982. Hemiptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 417-447. New York: McGraw-Hill Book Co.

Slipinski, S.A. 1988. Revision of the Australian Cerylonidae (Coleoptera: Cucujoidea). *Ann. Zool.*, 42: 1-74.

Sluss, T.P. and Foote, B.A. 1971. Biology and immature stages of *Leucopis verticalis* (Diptera: Chamaemyiidae). *Can. Entomol.*, 103: 1427-1434.

Smart, J. 1963. Explosive evolution and the phylogeny of insects. *Proc. Linn. Soc. London*, 174: 125-127.

Smetana, A. 1975. Revision of the New World genera of the Tribe Omicrini trib. nov. of the Hydrophilid Subfamily Sphaeridiinae (Coleoptera). *Stud. Neotrop. Fauna*, 10: 153-182.

Smit, F.G. 1982. Siphonaptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 557-563. New York: McGraw-Hill Book Co.

Smith, E.L. 1970. Biology and structure of some California bristletails and silverfish (Apterygota: Microcoryphia, Thysanura). *Pan-Pac. Entomol.*, 46: 212-225.

Smith, F.K. 1928. Larval characters of genus *Dixa*. *J. New York Entomol. Soc.*, 36: 263-284.

Smith, H.S. and Compere, H. 1928. A preliminary report on the insect parasites of the black scale, *Saissetia oleae* (Bern.). *Univ. California Publ. Entomol.*, 4: 231-334.

Smith, J.B. 1890. A contribution toward a knowledge of the mouth parts of the Diptera. *Trans. Am. Entomol. Soc.*, 17: 319-343.

Smith, J.B. 1892a. The mouth parts of *Copris carolina*: with notes on the homologies of the mandibles. *Trans. Am. Entomol. Soc.*, 19: 83-87, pls. 2-3.

Smith, J.B. 1892b. The structure of the hemipterous mouth. *Science*, 19: 189-190.

Smith, J.B. 1898. An essay on the development of the mouth parts of certain insects. *Trans. Am. Philos. Soc.*, N.S., 19: 175-198, pls. 1-3.

Smith, J.J.B. 1985. Feeding mechanisms. IN: Kerkut, G.A. and Gilbert, L.E., (Eds.), *Comprehensive Insect Physiology, Biochemistry, and Pharmacology*, 4: 33-85. Oxford: Pergamon Press.

Smith, K.G.V. 1986a. The faunal succession on cadavers. IN: Smith, K.G.V., *A Manual of Forensic Entomology*, pp. 13-35. London: British Museum of Natural History.

Smith, K.G.V. 1986b. Diptera. IN: Smith, K.G.V., *A Manual of Forensic Entomology*, pp. 68-137. London: British Museum of Natural History.

Smith, K.M. 1919. A comparative study of certain sense-organs in the antennae and palpi of Diptera. *Proc. Zool. Soc. London*, 1919: 31-69, pls. 1-4.

Smith, R.F. and Pritchard, A.E. 1956. Odonata. IN: Usinger, R.L., (Ed.), *Aquatic Insects of California, with Keys to North American Genera and California Species*, pp. 106-153. Berkeley: University of California Press.

Smithers, C.N. 1972. The classification and phylogeny of the Psocoptera. *Mem. Aust. Mus.*, 14: 1-349.

Smithers, C.N. 1982. Psocoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 394-406. New York: McGraw-Hill Book Co.

Snodgrass, R.E. 1905. A revision of the mouth-parts of the Corrodentia and the Mallophaga. *Trans. Am. Entomol. Soc.*, 31: 297-307.

Snodgrass, R.E. 1921. The mouth parts of the cicada. *Proc. Entomol. Soc. Washington*, 23: 1-15.

Snodgrass, R.E. 1922a. Mandible substitutes in the Dolichopodidae. *Proc. Entomol. Soc. Washington*, 23: 148-152.

Snodgrass R.E. 1922b. The resplendent shield-bearer and the ribbed-cocoon-maker: two insect inhabitants of the orchard. *Ann. Rept. Smithson. Inst.*, 1920: 485-509, pls. 1-3.

Snodgrass, R.E. 1928. Morphology and evolution of the insect head and its appendages. *Smithson. Misc. Collns.*, 81: 1-158.

Snodgrass, R.E. 1932. Evolution of the insect head and the organs of feeding. *Smithson. Rept.*, 1931: 443-489.

Snodgrass, R.E. 1935. *Principles of Insect Morphology*. New York: McGraw-Hill Book Co. 667 p.

Snodgrass, R.E. 1938a. The loral plates and the hypopharynx of Hemiptera. *Proc. Entomol. Soc. Washington*, 40: 228-236.

Snodgrass, R.E. 1938b. Evolution of the Annelida, Onychophora and Arthropoda. *Smithson. Misc. Collns.*, 97: 1-159.

Snodgrass, R.E. 1942. The skeleto-muscular mechanisms of the honey bee. *Smithson. Misc. Collns.*, 103: 1-120.

Snodgrass, R.E. 1943. The feeding apparatus of biting and disease-carrying flies: a wartime contribution to medical entomology. *Smithson. Misc. Collns.*, 104: 1-51.

Snodgrass, R.E. 1944. The feeding apparatus of biting and sucking insects affecting man and animals. *Smithson. Misc. Collns.*, 104: 1-113.

Snodgrass, R.E. 1946. The skeletal anatomy of fleas (Siphonaptera). *Smithson. Misc. Collns.*, 104: 1-89.

Snodgrass, R.E. 1947. The insect cranium and the "epicranial suture." *Smithson. Misc. Collns.*, 107: 1-52.

Snodgrass, R.E. 1950. Comparative studies on the jaws of mandibulate arthropods. *Smithson. Misc. Collns.*, 116: 1-85.

Snodgrass, R.E. 1953. The metamorphosis of a fly's head. *Smithson. Misc. Collns.*, 122: 1-25.

Snodgrass, R.E. 1954. The dragonfly larva. *Smithson. Misc. Collns.*, 123: 1-38.

Snodgrass, R.E. 1956. *The Anatomy of the Honey Bee*. Ithaca, N.Y.: Cornell University Press. 334 pp.

Snodgrass, R.E. 1959. The anatomical life of the mosquito. *Smithson. Misc. Collns.*, 139(8): 1-87.

Snodgrass, R.E. 1960. Facts and theories concerning the insect head. *Smithson. Misc. Collns.*, 142: 1-61.

Snodgrass, R.E. 1961. The caterpillar and the butterfly. *Smithson. Misc. Collns.*, 143: 1-51.

Snodgrass, R.E. 1963. A contribution toward an encyclopedia of insect anatomy. *Smithson. Misc. Collns.*, 146: 1-48.

Sokal, R.R. 1947. The anatomy of the head capsule of the dragonfly *Pantala flavescens* Fabricius. *Notes Entomol. Chin.*, 11: 157-223.

Solinas, M. 1968. Morfologia, anatomia e organizzazione funzionale del capo della larva matura di *Phaenobremia aphidimyza* (Rondani). *Entomologica*, 4: 1-44.

Sorg, M. 1986. Grabwespen der Gattung *Passaloecus* aus fossilen Harzen (Hymenoptera, Sphecoidea, Pemphredoninae). *Passaloecus microceras* n.sp., baltischer Bernstein, oberes Eozän, *Passaloecus munax* n.sp., Bitterfelder Bernstein, unteres Miozän. *Paläont. Z.*, 60: 277-284.

Southwood, T.R.E. 1973. The insect/plant relationship--an evolutionary perspective. IN: Van Emden, H.F., (Ed.), *Insect/Plant Relationships*, pp. 3-30. New York: John Wiley and Sons.

Southwood, T.R.E. 1978. The components of diversity. IN: Mound, L.A. and Waloff, N., (Eds.), "Diversity of Insect Faunas." *Symp. Roy. Entomol. Soc. London*, 9: 19-40. Oxford: Blackwell Scientific Publications.

Southwood, T.R.E. 1984. Insect-plant adaptations. *Ciba Found. Symp.*, 102: 138-151.

Spahr, U. 1988. Erganzungen und Berichtigungen zuk R. Keilbach's Bibliographie und Liste der Bernsteinfossilien--Uberordnung Hemipteroidea. *Stutt. Beitr. Naturk.*, (B), 144: 1-60.

Spence, J.R. and Sutcliffe, J.G. 1982. Structure and function of feeding in larvae of *Nebria* (Coleoptera: Carabidae). *Can. J. Zool.*, 60: 2382-2394.

Speyer, E.R. 1923. Researches upon the larch chermes (*Cnaphalodes strobilobius* Kalt.), and their bearing on the evolution of the Chermesinae in general. *Phil. Trans. Roy. Soc. London*, (B), 212: 111-146.

Spieth, H.T. 1933a. The phylogeny of some mayfly genera. *J. New York Entomol. Soc.*, 41: 55-86.

Spieth, H.T. 1933b. The phylogeny of some mayfly genera. Phylogenetic relations of genera. *J. New York Entomol. Soc.*, 41: 327-391.

Spooner, C.S. 1920. A note on the mouthparts of the Aradidae. *Ann. Entomol. Soc. Am.*, 13: 121-122.

Spooner, C.S. 1938. The phylogeny of the Hemiptera based on a study of the head capsule. *Illinois Biol. Mon.*, 16: 1-102.

Spradbury, J.P. 1973. *Wasps: An Account of the Biology and Natural History of Social and Solitary Wasps.* Seattle: University of Washington Press.

Srivastava, A.K. 1987. Lower Barakar flora of Raniganj Coalfield and insect/plant relationship. *The Palaeobotanist*, 36: 138-142.

Srivastava, K.P. 1957. On the morphology of lemon butterfly, *Papilio demoleus* (Lepidoptera). Part I. Skeleto-muscular mechanism (head and its appendages). *Proc. Natl. Acad. Sci. India*, 27: 115-128.

Srivastava, R.P. and Bogawat, J.K. 1969. Feeding mechanism of a fruit-sucking moth *Othreis materna* (Lepidoptera: Noctuidae). *J. Nat. Hist.*, 3: 165-181.

Staedler, E., 1977. Sensory aspects of insect/plant interactions. *Proc. 15th Int. Congr. Entomol.*, pp. 228-248.

Staesche, K. 1963. Ubersicht über die Fauna des deutschen Rotliegenden (Unteres Perm). *Stutt. Beit. Naturk.*, (B), 110: 1-6.

Stanford, J.A. and Ward, J.V. 1988. The hyporheic habitat of river ecosystems. *Nature*, 335: 64-66.

Stannard, L.J., Jr. 1956. Two new fossil thrips from Baltic amber (Thysanoptera, Terebrantia). *Fieldiana, Zool.*, 34: 453-460.

Stannard, L.J., Jr. 1968. The thrips, or Thysanoptera, of Illinois. *Bull. Illinois Nat. Hist. Surv.*, 29: 1-552.

Stannard, L.J., Jr. 1982. Thysanoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 415-417. New York: McGraw-Hill Book Co.

Starcke, K.P. 1949. Contribution to the biology of *Myrmica schencki* Em. (Hym., Form.). *Tijd. Entomol.*, 91: 25-71.

Statz, G. 1936. Ueber neue Funde von Neuropteren, Panorpaten und Trichopteren aus den tertiären Schiefern von Rott am Siebengebirge. *Decheniana*, 93: 208-255.

Statz, G. 1938. Tertiärschichten von Rott und ihre Wasserfauna. *Hemiat. Siegk.*, 3:

Statz, G. 1944a. Neue Dipteren (Nematocera) aus dem Oberoligocän von Rott. II. Familie: Fungivoridae (Pilzmücken). *Palaeontographica*, (B), 95: 13-19.

Statz, G. 1944b. Neue Dipteren (Nematocera) aus dem Oberoligocän von Rott. III. Familie Limnobiidae (Steltzmücken). IV. Familie Tipulidae (Schnaken). V. Familie Culicidae (Stechmücken). *Palaeontographica*, (B), 95: 93-121, pls. 20-24.

Statz, G. 1944c. Neue Dipteren (Nemnatocera) aus dem Oberoligocän von Rott. VI. Familie: Tendipedidae (Zuckoder Schwarmmücken). VII. Familie: Heleidae (Gnitzen). VIII. Familie: Lycoriidae (Trauermücken). *Palaeontographica*, (B), 95: 122-187, pls. 25-41.

Stebbing, E.P. 1910. A note on the lac insect (*Tachardia lacca*), its life history, propagation and collection. *Indian Forest Mem.*, 1: 1-82.

Stebbing, E.P. 1977. *Indian Forest Insects of Economic Importance: Coleoptera*. Bhopal: J.K. Jain Brothers. 648 p.

Steffan, A.W. 1964. Torridincolidae, coleopterorum nova familia e regione aethiopica. *Entomol. Z.*, 74: 193-200.

Steffan, A.W. 1968. Evolution und systematik der Adelgidae (Homoptera: Aphidina). *Zoologica*, 115: 1-139.

Steffan, W.A. 1981. Sciaridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 247-256.

Stein, J.P.E. 1877. Drei merkwürdige Bernstein Insekten. *Mitt. München Entomol. Ver.*, 1: 28-30.

Steinmann, H. and Zombori, L. 1981. *An Atlas of Insect Morphology*. Budapest: Akademiai Kiado. 248 pp.

Steinmann, H. and Zombori, L. 1984. *A Morphological Atlas of Insect Larvae*. Budapest: Akademiai Kiado. 403 pp.

Step, E. 1932. *Bees, Wasps, Ants and Allied Insects of the British Isles*. London: Frederick Warne & Co., Ltd. 238 pp.

Stephen, W.P., Bohart, G.E. and Torchio, P.F. 1969. *The Biology and External Morphology of Bees, with a Synopsis of the Genera of Northwestern America*. Corvallis: Oregon State University, Agricultural Experiment Station. 140 p.

Stephens, J.F. 1828a. *Illustrations of British Entomology; or a Synopsis of Indigenous Insects: Containing their Generic and Specific Distinctions; with an Account of the Metamorphoses, Times of Appearance, Localities, Food, and Economy, as far as Practable. Mandibulata. Volume 1*. London: Baldwin and Cradock. 188 pp.

Stephens, J.F. 1828b. *Illustrations of British Entomology; or a Synopsis of Indigenous Insects: Containing their Generic and Specific Distinctions; with an Account of their Metamorphoses, Times of Appearance, Localities, Food, and Economy, as far as Practicable. Haustellata. Volume 2*. London: Baldwin and Cradock. 152 pp.

Stephens, J.W.S. and Newstead, R. 1907. The anatomy of the proboscis of biting flies. Part II. *Stomoxys* (stable flies). *Ann. Trop. Med. Parasitol.*, 1: 171-198, pls. 12-19.

Sternfeld, R. 1907. Die Verkummerung der Mundteile und der Funktionswechsel des Darms bei den Ephemeriden. *Zool. Jb. (Anat.)*, 24: 415-430.

Stevens, G.C. 1983. *Atta cephalotes* (zompopas, leaf-cutting ants). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 688-691. Chicago: University of Chicago Press.

Stevenson, J.J. 1910. The coal basin of Commentry in central France. *Ann. New York Acad. Sci.*, 19: 161-204, 5 pls.

Steyskal, G.C. 1987. Dryomyzidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, 28: 923-926.

Steyskal, G.C. and Knutson, L.V. 1981. Dolichopodidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 607-624.

St. George, R.A. 1939. The larva *Perimylops anarcticus* Müller and the systematic position of the family Perimylopidae (Coleoptera). *Proc. Entomol. Soc. Washington*, 41: 207-214.

Stickney, F.S. 1923. The head-capsule of Coleoptera. *Illinois Biol. Mon.*, **8**: 1-105.

Stoffolano, J.G., Jr. and Yin, L.R.S. 1983. Comparative study of the mouthparts and associated sensilla of adult male and female *Tabanus nigrovittatus* (Diptera, Tabanidae). *J. Med. Entomol.*, **20**: 11-32.

Stojanovich, C.J., Jr. 1945. The head and mouthparts of the sucking lice (Insecta: Anoplura). *Microentomology*, **10**: 1-46.

Stone, A. 1964. Family Thaumaleidae. *Bull. Conn. Geol. Nat. Hist. Surv.*, **97**: 119-123.

Stone, A. 1981. Culicidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 341-350.

Stone, A. and Peterson, B.V. 1981. Thaumaleidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 351-354.

Stork, N.E. 1987. Guild structure of arthropods from Bornean rain forest trees. *Ecol. Entomol.*, **12**: 69-80.

Stöwe, E. 1943. Der Kopf von *Trimenopon jenningsi* Kellogg und Paine (Mallophaga), eine morphologische Untersuchung unter besonderer Berucksichtigung des Nervensystems und der Drusen. *Zool. Jb. (Anat.)*, **68**: 177-226.

Stradling, D.J. 1987. Nutritioinal ecology of ants. IN: Slansky, F. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates*, pp. 927-969. New York: John Wiley and Sons.

Straus, A. 1976. Eine Gangmine im Eocän von Messel. *Aufschluss*, **27**: 445-446.

Strenger, A. 1942. Funktionelle Analyse des Orthopterenkopfes. *Zool. Jb. (Syst.)*, **75**: 1-72.

Strenger, A. 1949. Funktionsstudie des Kopfes von *Forficula auricularia*. *Zool. Jb. (Anat.)*, **70**: 557-575.

Strenger, A. 1952. Die funktionelle und morphologische Bedeutung der Nahte am Insektenkopf. *Zool. Jb. (Anat.)*, **72**: 468-521.

Strenger, A. 1954. Zur Kopfmorphologie der Ephemeriden-larven. Erster Teil. *Ecdyonurus* und *Rithrogena*. *Oster. Zool. Z.*, **4**: 191-228.

Striganova, B.R. 1967. Morphological adaptations of the head and mandibles of some coleopterous larvae burrowing solid substrates. *Beitr. Entomol.*, 17: 639-649.

Strong, D.R., Lawton, J.H., and Southwood, T.R.E. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Cambridge, MA: Harvard University Press. 313 p.

Strümpel, H. 1983. Homoptera (Pflanzensauger). IN: Fischer, M., (Ed.), *Handbuch der Zoologie*, Band 4, Teilband 28: 1-218. Berlin: Walter de Gruyter.

Sturm, H. 1955. Beitrage zur Ethologie einiger mitteldeutscher Machiliden. *Z. Tierpsychol.*, 12: 337-363.

Sturm, H. 1959. Die Nahrung der Proturen. (Beobachtungen an *Acerentomon doderoi* Silv., und *Eosentomon transitorium* Berl.). *Naturwissenschaften*, 46: 90-91.

Sturm, H. 1984. Zur Systematik, Biogeographie und Evolution der südamerikanischen Meinertellidae (Machiloidea, Archaeognatha, Insecta). *Z. Zool. Syst. Evol.-Forsch.*, 22: 27-44.

Sturtevant, A.H. 1963. A fossil periscelid (Diptera) from the amber of Chiapas, Mexico. *J. Paleontol.*, 37: 121-122, pl. 16.

Stys, P. 1964. The morphology and relationship of the family Hyocephalidae (Heteroptera). *Acta Zool. Hung.*, 10: 229-262.

Stys, P. 1967. Medocostidae--a new family of cimicomorphan Heteroptera based on a new genus and two new species from tropical Africa. I. Descriptive part. *Acta Entomol. Bohemoslov.*, 64: 39-465.

Stys, P. 1969. On the morphology of the labrum in Heteroptera. *Acta Entomol. Bohemoslov.*, 66: 150-158.

Stys, P. 1970. On the morphology and classification of the family Dipsocoridae s. lat., with particular reference to the genus *Hypsipteryx* Drake (Heteroptera). *Acta Entomol. Bohemoslov.*, 67: 21-46

Subklew, W. 1938. Zur Morphologie der Larve von *Melolontha hippocastani* Fbr. *Arch. Naturges.*, N.F., 7: 270-304.

Suffolk, W.T. 1869. On the proboscis of the blow-fly. *Mon. Micros. J.*, 1: 331-342, pls. 15-17.

Sukacheva, I.D. 1968a. Mesozoic caddis flies (Trichoptera) of Transbaikalia. *Paleontol. J.*, 1968(2): 202-216.

Sukacheva, I.D. 1968b. New Jurassic caddisflies from Karatau (Trichoptera). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 175-179. Moscow: Academy of Science.

Sukacheva, I.D. 1973. New caddis-flies (Trichoptera) from the Mesozoic of Soviet central Asia. *Paleontol. J.*, 1973(3): 377-384.

Sukacheva, I.D. 1976. Caddis-flies of the suborder Permotrichoptera. *Paleontol. J.*, 1976(2): 198-209.

Sukacheva, I.D. 1980. Panorpida, Phryganeida, Papilionida. IN: Rohdendorf, B.B. and Rasnitsyn, A.P., (Eds.), "Historical Development of the Class Insecta." *Trans. Paleontol. Inst.*, **175**: 101-112. [In Russian.]

Sukacheva, I.D. 1982. Historical development of the order Phryganeida. *Trans. Paleontol. Inst.*, **197**: 1-111, pls. 1-8. [In Russian.]

Sundermeier, W. 1940. Der Hautpanzer des Kopfes und des Thorax von *Myrmeleon europaeus* und seine Metamorphose. *Zool. Jb. (Anat.)*, **66**: 291-348.

Surtees, G. 1959. Functional and morphological adaptations of the larval mouthparts in the sub-family Culicinae (Diptera) with a review of some related studies by Montschadsky. *Proc. Roy. Entomol. Soc. London*, (A), **34**: 7-16.

Suslov, S. 1912. Uber die Kopfdrusen einiger niederen Orthopteren. *Zool. Jb. (Anat.)*, **34**: 97-120.

Sutcliffe, J.F. 1985. Anatomy of membranous mouthpart cuticles and their roles in feeding in black flies (Diptera: Simuliidae). *J. Morphol.*, **186**: 53-86.

Sutcliffe, J.F. and Deepan, P.D. 1988. Anatomy and function of the mouthparts of the biting midge, *Culicoides sanguisuga* (Diptera: Ceratopogonidae). *J. Morphol.*, **198**: 363-365.

Sutcliffe, J.F. and McIver, S.B. 1984. Mechanics of blood-feeding in black flies (Diptera, Simuliidae). *J. Morphol.*, **180**: 125-144.

Suter, P.R. 1964. Biologie von *Echidnophaga gallinacea* (Westw.) und vergleich mit anderen verhaltenstypen bei flöhen. *Acta Trop.*, **21**: 193-238.

Sutton, M. 1947. Feeding mechanism of water-bugs. *Nature*, **160**: 122.

Suvarova, O.S. 1985. Use of morphology of mouth parts of horse-flies (Diptera, Tabanidae) in their systematics. IN: Skarlato, O.A., (Ed.), *Systematics of Diptera (Insecta): Ecological and Morphological Principles*, pp. 149-152. Leningrad: Academy of Sciences.

Swain, T. 1976. The effect of plant secondary products on insect/ plant coevolution. *Proc. 15th Int. Congr. Entomol.*, pp. 249-256.

Swaine, J.M. 1910. A new species of *Eccoptogaster*. *Can. Entomol.*, 42: 33-35, pl. 1.

Swan, L.A. and Papp, C.S. 1972. *The Common Insects of North America*. New York: Harper & Row, Publishers. 750 p.

Swan, L.W. 1961. The ecology of the high Himalayas. *Sci. Am.*, **205**: 68-78.

Sweet, M.H. 1979. On the original feeding habits of the Hemiptera (Insecta). *Ann. Entomol. Soc. Am.*, 72: 575-579.

Symmons, S. 1952. Comparative anatomy of the mallophagan head. *Trans. Zool. Soc. London*, 27: 349-436.

Szelegiewicz, H. and Popov, J.A. 1978. Revision der fossilen "Permaphidopsidae" aus dem Perm der UdSSR (Hemiptera: Sternorrhyncha). *Entomol. Germ.*, 4: 234-241.

Szent-Ivany, J.J.H., Womersley, J.S. and Ardley, J.H. 1956. Some insects of *Cycas* in New Guinea. *Papua New Guinea Agr. J.*, 11: 53-56.

Tabashnik, B.E. and Slansky, F., Jr. 1987. Nutritional ecology of forb foilage-chewing insects. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 71-103. New York: John Wiley and Sons.

Tahvanainen, J. and Niemelä, P. 1987. Biogeographical and evolutionary aspects of insect herbivory. *Ann. Zool. Fennici*, 24: 239-247.

Tanaka, Y. and Hisada, M. 1980. The hydraulic mechanism of the predatory strike in dragonfly larvae. *J. Exp. Biol.*, **88**: 1-19.

Tasch, P. 1957. Flora and fauna of the Rhynie Chert: a paleoecological re-evaluation of published evidence. *Bull. Univ. Wichita, Univ. Stud.*, 32: 1-23.

Tasch, P. and Zimmerman, J.R. 1959. New Permian insects discovered in Kansas and Oklahoma. *Science*, **130**: 1656.

Tasch, P. and Zimmerman, J.R. 1962. The *Asthenohymen-Delopterum* Bed --a new Leonardian insect horizon in the Wellington of Kansas and Oklahoma. *J. Paleontol.*, **36**: 1319-1333.

Tatchell, R.J. 1969. Host-parasite interactions and the feeding of blood-sucking arthropods. *Parasitology*, **59**: 93-104.

Tate, P. 1954. Notes upon the biology and morphology of the immature stages of *Neottiophilum praeustum* (Meigen, 1826) (Diptera: Neottiophilidae) parasitic on birds. *Parasitology*, **44**: 111-119.

Tauber, C.A. and Tauber, M.J. 1968. *Lomamyia latipennis* (Neuroptera: Berothidae) life history and larval descriptions. *Can. Entomol.*, **100**: 623-629.

Taylor, J.S. 1957. Notes on the proboscis in Lepidoptera. *Entomol. Rec.*, **69**: 25-29, 53-58.

Tedders, W.L. and Thompson, J.M. 1981. Histological investigation of stylet penetration and feeding damage to pecan foilage by three aphids (Hemiptera [Homoptera]: Aphididae). *Misc. Publ. Entomol. Soc. Am.*, **12**: 69-83.

Teixeira, C. 1954. La flore fossile des calcaires lithographiques de Santa Maria de Meya (Lérida, Espagne). *Bolm. Soc. Geol. Portugal*, **11**: 139-152.

Telenga, N.A. 1969. *Origin and Evolution of Parasitism in Hymenoptera Parasitica and Development of Their Fauna in the USSR.* Jerusalem: Israel Program for Scientific Translations. 112 p.

Teotia, T.P.S. 1964. The comparative morphology and anatomy of the last-instar larvae of *Bracon* (*Microbracon*) *gelechiae* Ashmead and *Apanteles flavipes* Cameron (Braconidae: Hymenoptera). *Ann. Zool.*, **4**: 73-112.

Terborgh, J. and Robinson, S. 1986. Guilds and their utility in ecology. IN: Kikkawa, J. and Anderson, D., (Eds.), *Community Ecology: Pattern and Process*, pp. 65-90. Oxford: Blackwell Scientific Publications.

Teskey, H.J. 1970. The immature stages and phyletic position of *Glutops rossi* (Diptera: Pelecorhynchidae). *Can. Entomol.*, **102**: 1130-1135.

Teskey, H.J. 1971. A new soldier fly from Canadian amber (Diptera: Stratiomyidae). *Can. Entomol.*, **103**: 1659-1661.

Teskey, H.J. 1976. Diptera larvae associated with trees in North America. *Mem. Entomol. Soc. Canada*, **100**: 1-53.

Teskey, H.J. 1981a. Pelecorhynchidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 459-462.

Teskey, H.J. 1981b. Nemestrinidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 585-588.

Teskey, H.J. 1981c. Vermileonidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 529-532.

Teskey, H.J. 1981d. Key to families--larvae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 125-147.

Teskey, H.J., 1981e. Morphology and terminology--larvae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch, Agr. Canada*, **27**: 65-88.

Teskey, H.J. 1987. Aulacigastridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **28**: 891-894.

Teskey, H.J. 1984. Aquatic Diptera, part one. Larvae of aquatic Diptera. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 448-466. Dubuque, IA: Kendall/Hunt Publ. Co.

Tetley, H. 1918. The structure of the mouth-parts of *Pangonia longirostris* in relation to the probable feeding-habits of the species. *Bull. Entomol. Res.*, **8**: 253-267.

Théobald, N. 1937. Note complémentaire sur les insectes fossiles Oligocènes des gypses d'Aix-en-Provence. *Bull. Mens. Soc. Sci. Nancy*, **6**: 157-178, pls. 1-2.

Theron, J.G. 1958. Comparative studies on the morphology of male scale insects (Hemiptera: Coccoidea). *Ann. Univ. Stellenbosch*, (A), **34**: 1-71.

Theron, J.G. 1962. Structure and relationships of the male of *Phenacoleachia zealandica* (Maskell) (Hemiptera: Coccoidea). *Proc. Roy. Entomol. Soc. London*, (A). **37**: 145-153.

Theron, J.G. 1968. Studies on the morphology and relationships of male Apiomorpha and *Opisthoscelis* (Hemiptera: Coccoidea). *Aust. J. Zool.*, **16**: 87-99.

Thien, L.B. 1969. Mosquito pollination of *Habenaria obtusata* (Orchidaceae). *Am. J. Bot.*, **56**: 232-237.

Thien, L.B. 1980. Patterns of pollination in the primitive angiosperms. *Biotropica*, **12**: 1-13.

Thien, L.B., et al. 1985. The pollination of *Zygogynum* (Winteraceae) by a moth, *Sabatinca* (Micropterygidae): an ancient association? *Science*, **227**: 540-543.

Thieroff, W.R. 1928. The economic importance of *Paratenodera sinensis*. *Entomol. News*, **39**: 140-145.

Thomas, I., 1933. On the bionomics and structure of some dipterous larvae infesting cereals and grasses. I. *Opomyza florum* Fabr. *Ann. Appl. Biol.*, **20**: 707-721.

Thomas, I., 1934. On the bionomics and structure of some dipterous larvae infesting cerals and grasses. II. *Opomyza germinationis* L. *Ann. Appl. Biol.*, **21**: 519-529.

Thomas, I., 1938. On the bionomics and structure of some dipterous larvae infesting cereals and grasses. III. *Geomyza* (*Balioptera*) *tripunctata* Fall. *Ann. Appl. Biol.*, **25**: 181-196.

Thomas, J.G. 1966. The sense organs on the mouth parts of the desert locust (*Schistocerca gregaria*). *J. Zool.*, **148**: 420-448.

Thomas, R.D.K. 1979. Morphology, constructional. IN: Fairbridge, R.W. and Jablonski, D., *The Encyclopedia of Paleontology*, pp. 482-487. Stroudsberg, PA: Dowden, Hutchinson and Ross, Inc.

Thompson, W.R. and Parker, H.L. 1930. The morphology and biology of *Eulimneria crassifemur*, an important parasite of the European corn borer. *J. Agr. Res.*, **40**: 321-345.

Thomson, A.J. 1977. The mechanics of proboscis extension by the blowfly *Phormia regina* Meigen. *Can. J. Zool.*, **55**: 602-606.

Thorpe, W.H. 1941. The biology of *Cryptochaetum* (Diptera) and *Eupelmus* (Hymenoptera) parasites of *Aspidoproctus* (Coccidae) in east Africa. *Parasitology*, **33**: 149-168.

Tichomirova, A. 1968. Jurassic staphylinid-beetles from Karatau. IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 139-154. Moscow: Academy of Sciences. [In Russian.]

Tiegs, O.W. 1940. The embryology and affinities of the Symphyla, based on a study of *Hanseniella agilis*. *Quart. J. Micros. Sci.*, **82**: 1-225.

Tiffney, B.H. 1981. Diversity and major events in the evolution of land plants. IN: Niklas, K.J., (Ed.), *Paleobotany, Paleoecology and Evolution*, 2: 193-230. New York: Praeger Publishers.

Tillyard, R.J. 1916. Mesozoic and Tertiary insects of Queensland and New South Wales. *Queensland Geol. Surv. Publ.*, 253: 1148.

Tillyard, R.J. 1917a. *The Biology of Dragonflies*. Dragonflies. Cambridge: Cambridge Univ. Press. 396 pp.

Tillyard, R.J. 1917b. Mesozoic insects of Queensland. No. 1. Planipennia, Trichoptera, and the new order Protomecoptera. *Proc. Linn. Soc. New South Wales*, 42: 175-200, pls. 7-9.

Tillyard, R.J. 1918. Mesozoic insects of Queensland. No. 3. Odonata and Protodonata. *Proc. Linn. Soc. New South Wales*, 43: 417-436.

Tillyard, R.J. 1919. Mesozoic insects of Queensland. No. 5. Mecoptera, the new order Paratrichoptera, and additions to the Planipennia. *Proc. Linn. Soc. New South Wales*, 44: 194-212.

Tillyard, R.J. 1921. Studies of New Zealand Trichoptera or caddisflies: No. 1, description of a new genus and species belonging to the family Sericosomatidae. *Trans. New Zealand Inst.*, 53: 346-350.

Tillyard, R.J. 1922. Mesozoic insects of Queensland. No. 9. Orthoptera and additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. *Proc. Linn. Soc. New South Wales*, 47: 447-470, pls. 51-53.

Tillyard, R.J. 1923a. The life-history of the Australian moth-lacewing, *Ithone fusca*, Newman (Order Neuroptera Planipennia). *Bull. Entomol. Res.*, 13: 205-223.

Tillyard, R.J. 1923b. On the mouth-parts of the Micropterygoidea. *Trans Entomol. Soc. London*, 1923: 181-206.

Tillyard, R.J. 1923c. Mesozoic insects of Queensland. No. 10. Summary of the Upper Triassic insect fauna of Ipswich, Q. (With an appendix describing new Hemiptera and Planipennia). *Proc. Linn. Soc. New South Wales*, 48: 481-498, pl. 43.

Tillyard, R.J. 1925a. The British Liassic dragonflies. *Brit. Mus. (Nat. Hist.), Fossil Insects*, 1: 1-40, pls. 1-5.

Tillyard, R.J. 1925b. Kansas Permian insects. No. 4. The orders Protodonata and Odonata. *Am. J. Sci.*, (5), 10: 41-73.

Tillyard, R.J. 1926a. *The Insects of Australia and New Zealand*. Sydney: Angus and Robertson, Ltd. 560 p.

Tillyard, R.J. 1926b. Kansas Permian insects. Part 7. The order Mecoptera. *Am. J. Sci.*, (5), 11: 133-164.

Tillyard, R.J. 1926c. Kansas Permian insects. Part 8. The order Copeognatha. *Am. J. Sci.*, (5), 11: 313-349.

Tillyard, R.J. 1926d. Upper Permian insects of New South Wales. Part II. The orders Mecoptera, Paramecoptera, and Neuroptera. *Proc. Linn. Soc. New South Wales*, 51: 265-282, pls 15-16.

Tillyard, R.J. 1928a. Some remarks on the Devonian fossil insects from the Rhynie Chert beds, Old Red Sandstone. *Trans. Entomol. Soc. London*, 76: 65-71.

Tillyard, R.J. 1928b. Kansas Permian insects. Part 10. The new order Protoperlaria: a study of the typical genus *Lemmatophora* Sellards. *Am. J. Sci.*, (5), 16 185-220.

Tillyard, R.J. 1932a. Kansas Permian insects. Part 14. The order Neuroptera. *Am. J. Sci.*, (5), 23: 1-30.

Tillyard, R.J. 1932b. Kansas Permian insects. Part 15. The order Plectoptera. *Am. J. Sci.*, (5), 23: 97-134.

Tillyard, R.J. 1933. The Panorpoid Complex in the British Rhaetic and Lias. *Brit. Mus. (Nat. Hist.), Fossil Insects*, 3: 1-79, pl. 1.

Tillyard, R.J. 1935a. Evolution of scorpion-flies and their derivatives (Order Mecoptera). *Ann. Entomol. Soc. Am.*, 28: 1-45.

Tillyard, R.J. 1935b. Upper Permian insects New South Wales. Part V. The order Perlaria or stoneflies. *Proc. Linn. Soc. New South Wales*, 60: 385-391.

Tillyard, R.J. 1937. Kansas Permian insects. Part 17. The order Megasecoptera and additions to the Palaeodictyoptera, Odonata, Protoperlaria, Copeognatha and Neuroptera. *Am. J. Sci.*, (5), 33: 81-110.

Timon-David, J. 1943. Insectes fossiles de l'Oligocene inferieur des Camoins (Bassin de Marseille). I. Diptères Brachycères. *Bull. Soc. Entomol. France*, 9:128-134.

Tindale, N.B. 1945. Triassic insects of Queensland. 1. *Eoses*, a probable lepidopterous insect from the Triassic beds of Mt. Crosby, Queensland. *Proc. Roy. Soc. Queensland*, 56: 37-46, pl. 5.

Tindale, N.B. 1980. Origin of the Lepidoptera, with description of a new mid-Triassic species and notes on the origin of the butterfly stem. *J. Lepid. Soc.*, 34: 263-285.

Ting, P.C. 1933. Feeding mechanisms of weevils, their function, and relationship to classification. *California Dept. Agr. Mo. Bull.*, 22: 161-165.

Ting, P.C. 1936. The mouth parts of the coleopterous group Rhynchophora. *Microentomology*, 1: 93-114.

Tjallingii, W.F. 1978. Mechanoreceptors of the aphid labium. *Entomol. Exp. Appl.*, 24: 531-537.

Tokunaga, M. 1932. A remarkable dipterous insect from Japan, *Nymphiomyia alba* gen. et sp. nov. *Annotes Zool. Japan*, 13: 559-569.

Tokunaga, M. 1935. A morphological study of a nymphomyiid fly. *Philip. J. Sci.*, 56: 127-214, pls. 1-5.

Torre-Bueno, J.R. 1985. *A Glossary of Entomology, with Supplement.* New York: New York Entomological Society. 390 p.

Tosi, A. 1896. Di un nuovo genere di Apiaria fossile nell'ambra di Sicilia (*Meliponorytes succini-M. sicula*). *Riv. Ital. Paleontol.*, 3: 352-356.

Tower, D.G. 1913. The external anatomy of the squash bug, *Anasa tristis* De G. *Ann. Entomol. Soc. Am.*, 6: 427-437.

Tower, D.G. 1914. The mechanism of the mouth parts of the squash bug, *Anasa tristis* tristis DeGeer. *Psyche*, 21: 99-108.

Townes, H. 1973a. Two ichneumonids (Hymenoptera) from the Early Cretaceous. *Proc. Entomol. Soc. Washington*, 75: 216-219.

Townes, H. 1973b. Three tryphonine ichneumonids from Cretaceous amber (Hymenoptera). *Proc. Entomol. Soc. Washington*, 75: 283-287.

Tragardh, I. 1913. Contributions towards the comparative morphology of the trophi of the lepidopterous leaf-miners. *Arkiv Zool.*, 8: 1-48.

Traub, R. 1980a. Some adaptive modifications in fleas. IN: Traub, R. and Starcke, H., (Eds.), *Fleas*, pp. 33-67. Rotterdam: Balkema.

Traub, R. 1980b. The zoogeography and evolution of some fleas, lice and mammals. IN: Traub, R. and Starcke, H. (Eds.), *Fleas*, pp. 93-172. Rotterdam: A.A. Balkema.

Traub, R., Rothschild, M. and Haddow, J.F. 1983. *The Rothschild Collection of Fleas. The Ceratophyllidae: Key to the Genera and Host Relationships.* London: Academic Press. 288 p.

Traxler, F.E. 1977. Developmental anatomy of the cephalopharyngeal apparatus of the first and second instars of *Lucilia serricata* (Meigen) larva (Diptera: Calliphoridae). *J. New York Entomol. Soc.*, 85: 2-17.

Tribout, P. 1956. Contribution a l'etude des jassides. *Trav. Lab. Zool., Univ. Dijon*, 16: 1-32, figs. 1-46.

Triggiani, O. 1978. La *Microsetia sexgutella* Thunberg (Lepidoptera: Gelechiidae) microlepidottero minatore delle foglie di *Chenopodum album* L. *Entomologica*, 14: 9-24.

Trombetta, L.D. 1976. Musculature of the head appendages *Tenebrio molitor* (Coleoptera: Tenebrionidae). *Ann. Entomol. Soc. Am.*, 69: 671-676.

Tröster, G. 1987. Skelet und Muskulatur des Kopfes der Larve von *Pterostichus nigrita* (Paykull) (Coleoptera: Carabidae). *Stutt. Beit. Naturk.*, 399: 1-23.

Tuxen, S.L. 1959. The phylogenetic significance of entognathous apterygotes. *Smithson. Misc. Collns.*, 137: 379-416.

Tuxen, S.L. 1962. Vermutete aussere Anzeichen einer Kopfsegmentierung bei den Arthropoden. *Zool. Anz.*, 169: 468-480.

Tuxen, S.L. 1967. The entomologist, J.C. Fabricius. *Ann. Rev. Entomol.*, 12: 1-14.

Tuxen, S.L. 1971. All Apterygota are true insects with no symphylan connection. *Proc. 13th Int. Congr. Entomol.*, 1: 311-312.

Tuxen, S.L. 1973. Entomology systematizes and describes: 1700-1815. IN: Smith, R.F., Mittler, T.E. and Smith, C.N., (Eds.), *History of Entomology*, pp. 95-118. Palo Alto, CA: Annual Reviews, Inc.

Uhler, P.R. 1884. Order VI. Hemiptera: sub-order III--Heteroptera. *Standard Natural History* 2: 249-296.

Ulmer, G. 1905. Uber einige Trichopteren mit russelformigen Kopfanhangen. *Zool. Anz.*, 28: 56-59.

Ulmer, G. 1912. Die Trichopteren des baltischen Bernsteins. *Beit. Naturk. Preussens*, 10: 1-380.

Ulrich, W. 1924. Die Mundwerkzeuge der Spheciden (Hym, Foss.). Beitrag zur Kenntnis der Insketenmundwerkzeuge. *Z. Morphol. Okol. Tiere*, 1: 539-636.

Ulrich, W. 1927. Uber das bisher einzige Strepsipteron aus dem baltischen Bernstein und über Theorie der Mengeinenbiologie. *Z. Morphol. Okol. Tiere*, 8: 45-62.

Ulrich, W. 1943. Die Mengeidae (Mengenillini) und die Phylogenie der Strepsipteren. *Z. Parasitenk.*, 13: 62-101.

Ussatchov, D.A. 1968. New Jurassic Asilomorpha (Diptera) of the Karatau. *Entomol. Rev.*, 47: 378-384.

Usinger, R.L., (Ed.), 1956. *Aquatic Insects of California, with Keys to North American Genera and California Species*. Berkeley: Univ. California Press. 508 p.

Usinger, R.L. 1956. Aquatic Hemiptera. IN: Usinger, R.L., (Ed.), *Aquatic Insects of California, with Keys to North American Genera and California Species*, pp. 182-228. Berkeley: University of California Press.

Uvarov, B.P. 1928. Insect nutrition and metabolism: a summary of the literature. *Trans. Entomol. Soc. London*, 76: 255-343.

Uvarov, B.P. 1966. *Grasshoppers and Locusts*. Cambridge: Cambridge Univ. Press.

Vaillant, F. and Delhom, M.M. 1956. Les formes adaptatives de l'appareil bucco-pharyngien chez les larves de Stratiomyiidae (Diptera). *Bull. Soc. Hist. Nat. Afr. Nord*, 47: 217-250.

Val, F.C. 1976. Systematics and evolution of the Pantophthalmidae (Diptera, Brachycera). *Arq. Zool.*, 27: 51-164.

Valley, K., Novak, J.A., and Foote, B.A. 1969. Biology and immature stages of *Emetopiella rufipes*. *Ann. Entomol. Soc. Am.*, 62: 227-234.

Van Amerom, H.W.J. 1966. *Phagophythichnus ekowskii* nov. ichnogen. & nov. ichnosp., eine missbildung infolge von Insektenfrass, aus dem Spanischen Stephanien (Provinz Léon). *Leidse Geol Meded.*, 38: 181-184, pls. 1-3.

Van Amerom, H.W.J. and Boersma, M. 1971. A new find of the icnhofossil *Phagophytichnus ekowskii* Van Amerom. *Geol. Mijn.*, 50: 667-670.

Vance, A.M. and Smith, H.D. 1933. The larval head of parasitic Hymenoptera and nomenclature of its parts. *Ann. Entomol. Soc. Am.*, 26: 86-94.

Van der Meijden, E., Wijn, M. and Verkaar, H.J. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos*, 51: 355-363.

Van Embden, H.F. 1978. Insects and secondary plant substances--an alternative viewpoint with special reference to aphids. IN: Harborne, J.B., (Ed.), *Biochemical Aspects of Plant and Animal Coevolution*, pp. 309-323. London: Academic Press.

Vanin, S.A. 1976. Taxonomic revision of the South American Belidae (Coleoptera). *Arq. Zool.*, 28: 1-75.

Van Valen, L. 1971. Adaptive zones and the orders of mammals. *Evolution*, 25: 420-428.

Vargas, M. and Fallas, F. 1983. *Simulium* (mosca de cafe, mosca negra, black fly). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 769-770. Chicago: University of Chicago Press.

Vassal, M.-A. 1947. Recherches sur l'hypopharynx des éphémeres. *Bull. Scient. Bourgogne*, 8: 133-140.

Vasudeva, S. 1956. Studies on the morphology of the common lemmon butterfly, *Papilio demoleus demoleus* L. *J. Zool. Soc. India*, 8: 211-234.

Veeresh, G.K. and Kumari, K.V. 1985. Behavioural analysis of feeding and breeding in lamellicorn beetles. *Proc. Indian Acad. Sci. (Anim. Sci.)*, 94: 303-308.

Velayudhan, R. and Annadurai, R.S. 1986. Pollination potential of thrips (Insecta: Thysanoptera) in some solanaceous plants. *Proc. Indian Acad. Sci. (Acad. Sci.)*, 95: 109-116.

Venables, E.M. and Taylor, H.E. 1962. An insect fauna of the London Clay. *Proc. Geol. Assn.*, 73: 273-279, pl. 12.

Verhoef, H.A., Prast, J.E. and Verweij, R.A. 1988. Relative importance of fungi and algae in the diet and nitrogen nutrition of *Orchesella cincta* (L.) and *Tomocerus minor* (Lubbock) (Collembola). *Funct. Ecol.*, 2: 195-201.

Verhoeff, K.W. 1923. Beitrage zur Kenntnis der Coleopteren-Larven mit besonderer Bearucksichtigung der Clavicornia. *Arch. Naturges.*, (A), 89: 1-109.

Verma, S.R., Tyagi, M.P. and Gupta, S.P. 1973. Studies on the morphology of *Belostoma indicus* Lep. et Serv. (head capsule and mouth parts. *Zool. Jb. (Anat.)*, 91: 449-463.

Vermeij, G.J. 1987. *Evolution and Escalation: An Ecological History of Life*. Princeton: Princeton University Press. 527 p.

Vickery, V.R. 1989. The biogeography of Canadian Grylloptera and Orthoptera. *Can. Entomol.*, 121: 389-424.

Vishniakova, V.N. 1968. Mesozoic cockroaches with an external ovipositor and the specific features of their reproduction (Blattoidea). IN: Rohdendorf, B.B., (Ed.), *Jurassic Insects of Karatau*, pp. 55-86. Moscow: Academy of Sciences. [In Russian.]

Vishniakova, V.N. 1973. New cockroaches (Insecta, Blattoidea) from the Upper Jurassic deposits of the Karatau Montains. *Dokl. 24th Ann. Lect. Memory N.A. Kholodkovskogo*, 24: 64-77. [In Russian.]

Vishniakova, V.N. 1975. Psocoptera in Late Cretaceous insect-bearing resins from the Taimyr. *Entomol. Rev.*, 54: 63-75.

Vishniakova, V.N. 1976. Relict Archipsyllidae (Insecta, Psocoptera) in the Mesozoic fauna. *Paleontol. J.*, 1976(2): 180-188.

Vishniakova, V.N. 1981. New Paleozoic and Mesozoic lophoneurids (Thripida, Lophioneuridae). *Trans. Paleontol. Inst.*, 183: 43-63, pls. 14-15.

Vinson, S.B. and Barbosa, P. 1987. Interrelationships of nutritional ecology of parasitoids. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*, pp. 673-695. New York: John Wiley and Sons.

Vishnoi, H.S. 1956. The structure, musculature and mechanism of the feeding apparatus of the various castes of the termite *Odontotermes obesus* (Rambur). *J. Zool. Soc. India*, 8: 1-18.

Vit, S. 1977. Contribution a la conaissance des Eucinetidae (Coleoptera). *Rev. Suisse Zool.*, 84: 917-935.

Vit, S. 1981. Une novelle espece du genre *Tohlezkus* Vit de Taiwan (Coleoptera, Eucinetidae). *Rev. Suisse Zool.*, 88: 669-774.

Vockeroth, J.R. 1981. Mycetophilidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 223-246.

Vockeroth, J.R. 1987a. Opomyzidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, 28: 881-885.

Vockeroth, J.R. 1987b. Anthomyzidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, **28**: 887-890.

Vockeroth, J.R. 1987c. Scathophagidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, **28**: 1085-1097.

Vockeroth, J.R. and Peterson, B.V. 1987. Syrphidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, **28**: 713-743.

Vogel, R. 1915. Beitrag zur Kenntnis des Baues und der Lebensweise der Larve von *Lampyris noctiluca*. *Z. Wiss. Zool.*, **112**: 291-432.

Vogel, R. 1920. Zur Anatomie des Stechrussels von *Glossina fusca* Walk. *Zool. Anz.*, **51**: 269-279.

Vogel, R. 1921. Kritische und erganzende Mitteilungen zur Anatomie des Stechapparats der Culiciden und Tabaniden. *Zool. Jb. (Anat.)*, **42**: 259-282.

Voigt, E. 1938. Weichteile an fossilen Insekten aus der eozänen Braunkohle des Geiseltales bei Halle Saale. *Nova Acta Leop.*, N.F., **6**: 1-38, pls. 1-7.

Voigt, E. 1952. Ein Haareinschluss mit Phthiarapteren-Eiern im Bernstein. *Mitt. Geol. Inst Hamburg*, **21**: 59-74.

Voss, E. 1953. Einige Rhynchophoren der Bernsteinfauna (Col.). *Mitt. Geol. Staatinst. Hamburg*, **22**: 119-140.

Voss, E. 1972. Einige Rüsselkäfer der Tertiärzeit aus baltischen Bernstein (Coleoptera, Curculionoidea). *Steenstrupia*, **2**: 167-181.

Waage, J.K. 1979. The evolution of insect/vertebrate associations. *Biol. J. Linn. Soc.*, **12**: 187-224.

Wada, S. 1965. Analyse der Kopf-Hals-Region von *Tachycines* (Saltatoria) in morphogenetische Einheiten. I. Miteilung: Anatomische Befunde im schlupfreifen und im imaginalen Normalzustand. *Zool. Jb. (Anat.)*, **83**: 185-234.

Waddington, K.D. 1987. Nutritional ecology of bees. IN: Slansky, F., Jr. and Rodriguez, J.G., (Eds.), *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates*, pp. 393-419. New York: John Wiley and Sons.

Wagner, H. 1924. Ein neues *Apion* aus dem baltischen Bernstein. *Deut. Entomol. Z.*, 1924: 134-136.

Waldbauer, G.P. 1962. The mouth parts of female *Psorophora ciliata* (Diptera, Culicidae) with a new interpretation of the functions of the labral muscles. *J. Morphol.*, 111: 201-215.

Waldbauer, G.P. 1968. The consumption and utilization of food by insects. IN: Beament, J.W.L., Treherne, J.E. and Wigglesworth, V.B., (Eds.), *Advances in Insect Physiology*, pp. 229-288. New York: Academic Press.

Walker, E.M. 1931a. On the clypeus and labium of primitive insects. *Can. Entomol.*, 58: 75-81.

Walker, E.M. 1931b. On the anatomy of *Grylloblatta campodeiformis* Walker. 1. Exoskeleton and musculature of the head. *Ann. Entomol. Soc. Am.*, 24: 519-536.

Walker, E.M. 1932. Prognathism and hypognathism in insects. *Can. Entomol.*, 44: 223-229.

Walker, E.M. 1933. On the anatomy of *Grylloblatta campodeiformis* Walker. 2. Comparisons of head with those of other orthopteroid insects. *Ann. Entomol. Soc. Am.*, 24: 309-344.

Walker, E.M. 1937. *Grylloblatta*, a living fossil. *Trans. Roy. Soc. Canada*, (3), 26: 1-10.

Walker, G.P. 1985. Stylet penetration by the bayberry whitefly, as affected by leaf age in lemon, *Citrus limon*. *Entomol. Exp. Appl.*, 39: 115-121.

Walker, J.W. and Walker, A.G. 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. *Ann. Missouri Bot. Gard.*, 71: 464-521.

Walker, M.V. 1938. Evidence of Triassic insects in the Petrified Forest National Monument, Arizona. *Proc. U.S. Natl. Mus.*, 85: 137-141, pls. 1-4.

Walker, T.L. 1934. Chemawinite or Canadian amber. *Univ. Toronto Stud. Geol.*, 36: 5-10, pls. 1-2.

Wallace, J.B. and Malas, D. 1976. The fine structure of capture nets of larval Philopotamidae (Trichoptera) with special emphasis on *Dolophilodes distinctus*. *Can. J. Zool.*, 54: 1788-1802.

Wallace, J.B. and Merritt, R.W. 1980. Filter-feeding ecology of aquatic insects. *Ann. Rev. Entomol.*, 25: 103-132.

Walshe, B.M. 1947. Feeding mechanisms of *Chironomus* larvae. *Nature*, 160: 474.

Walshe, B.M. 1951. The feeding habits of certain chironomid larvae. *Proc. Zool. Soc. London*, 121: 63-79.

Walter, A. 1885a. Palpus maxillaris lepidopterorum. *Jen. Z. Naturwiss.*, N.S., 19: 121-173, pl. 15.

Walter, A. 1885b. Beitrage zur Morphologie der Schmetterlinge. *Jen. Z. Naturwiss.*, N.S., 19: 751-807, pls. 23-24.

Walther, J. 1904. Die Fauna der Solnhofener Plattenkalke bionomisch betrachtet. *Jen. Denkschr. Med. Naturwiss. Ges.*, 11: 135-214.

Warren, A. 1915. A study of the food habits of Hawaiian dragonflies. *Coll. Hawaii Publ. Bull.*, 3: 1-45.

Waterhouse, C.O. 1893. Some observations on the mouth-parts of Diptera. *Ann. Mag. Nat. Hist.*, 11: 45-46.

Waters, S.B. 1989a. A Cretaceous dance fly (Diptera: Empididae) from Botswana. *Syst. Entomol.*, 14: 233-241.

Waters, S.B. 1989b. A new hybotine dipteran from the Cretaceous of Botswana. *Palaeontology*, 32: 657-667.

Watson, M.C. 1955. The utilization of mandibular armature in taxonomic studies of anisopterous nymphs. *Trans. Entomol. Soc. Am.*, 81: 155-205.

Watt, J.C. 1970. Coleoptera: Perymylopidae of South Georgia. *Pac. Insects Mon.*, 23: 243-253.

Watt, J.C. 1974. Chalcodryidae: a new family of heteromerous beetles (Coleoptera: Teneobrionoidea). *J. Roy. Soc. New Zealand*, 4: 19-38.

Webb, J.A. 1982. Triassic species of *Dictyophyllum* from eastern Australia. *Alcheringa*, 6: 79-91.

Weber, H. 1928. Zur vergleichenden Physiologie der Saurorgane der Hemipteren mit besonderer Berucksichtigung der Pflanzenlause. *Z. Vergl. Physiol.*, 8: 145-186.

Weber, H. 1929. Kopf und Thorax von *Psylla mali* Schmidb. (Hemiptera --Homoptera): eine morphogenetische Studie. *Z. Morphol. Okol. Tiere*, 14: 59-165.

Weber, H. 1930. *Biologie der Hemipteren: Eine Naturgeschichte der Schnabelkeife*. Berlin: Julius Springer. 543 p.

Weber, H. 1933. *Lehrbuch der Entomologie*. Jena. 726 p.

Weber, H. 1936. Copeognatha. IN: Schulze, H., *Biologie der Tiere Deutschlands*, Lfg. 39, Teil 27: 1-50. Berlin.

Weber, H. 1938a. Beitrage zur Kenntnis der Uberordnung Psocoidea. 1. Die labialdrusen der Copeognathen. *Zool. Jb. (Anat.)*, 64: 243-286.

Weber, H. 1938b. Beitrage zur Kenntnis der Uberordnung Psocoidea. 4. Ein neues Organ im Kopf der Elefantlaus *Haematomyzus elephantis* Piaget. *Zool. Anz.*, 124: 97-103.

Wedde, H. 1885. Beiträge zur Kenntniss des Rhynchotenrüssels. *Arch. Naturges.*, 51: 113-143.

Weiczorek, H. 1973. Zur Kenntnis der Alderfarninsekten: Ein Beitrag zum Problem der biologischen Dekaemfung von *Pteridium aquilinum* (L.) Kuhn im Mitteleuropa. *Z. Angew. Entomol.*,72: 337-358.

Weinreich, E. 1968. Uber den Klebfangapparat der Imagines von *Stenus* Latr. (Coleopt., Staphylinidae) mit einem Beitrag zur Kenntnis der Jugenstadien dieser Gattung. *Z. Morphol. Okol. Tiere*, 62: 162-310.

Weiss, F.E. 1904. A probable parasite of stigmarian rootlets. *New Phytol.*, 3: 63-68.

Weller, S.J. 1987. *Litodonta hydromeli* Harvey (Notodontidae): description of life stages. *J. Lepid. Soc.*, 41: 187-194.

Wenk, P. 1953. Der Kopf von *Ctenocephalus canis* (Curt.) (Aphaniptera). *Zool. Jb. (Anat.)*, 73: 103-164.

Wenk, P. 1961. Die Muskulatur der Mandibel einiger blutsaugender Culiciden. *Zool. Anz.*, 167: 254-259.

Wenk, P. 1962. Anatomie des Kopfes von *Wilhelmia equina* equina L. (Simuliidae syn. Melusinidae, Diptera). *Zool. Jb. (Anat.)*, 80: 81-134.

Wenk, P. 1980. How bloodsucking insects perforate the skin of their hosts. IN: Traub, R. and Starcke, H., (Eds.), *Fleas*, pp. 329-335. Rotterdam: A.A. Balkema.

Wenk, P. and Schlorer, G. 1963. Wirtsorientierung und Kopulation bei blutsaugenden Simuliiden (Diptera). *Z. Tropenmed. Parasitol.*, 14: 177-191.

Wensler, R.J. and Filshie, B.K. 1969. Gustatory sense organs in the food canal of aphids. *J. Morphol.*, 129: 473-492.

Wenzel, R.L. and Peterson, B.V. 1987. Streblidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 2. *Res. Branch Agr. Canada*, **28**: 1293-1301.

Werner, K. 1958. Die Larvalsystematik einiger Kleinschmetterlingsfamilien (Hyponomeutidae, Orthoteliidae, Acrolepiidae, Tineidae, Incurvariidae und Adelidae). *Abh. Larvalsyst. Ins.*, 2: 1-145.

Weschè, W. 1902. Undescribed palpi on the proboscis of some dipterous flies, with remarks on the mouth-parts in several families. *J. Roy. Micros. Soc.*, **1902**: 412-416, pls. 9-10.

Weschè, W. 1904. The labial and maxillary palpi in Diptera. *Trans. Linn. Soc. London*, **9**: 219-230, pls. 8-10.

Weschè, W. 1908. The proboscis of the blow-fly, *Calliphora erythrocephala*, Mg.--a study in evolution. *J. Queckett Micros. Club*, 10: 283-294, pls. 22, 23.

Weschè, W. 1909. The mouth-parts of the Nemocera and their relations to the other families in Diptera. Corrections and additions to the paper published in 1904. *J. Roy. Micros. Soc.*, **1909**: 1-16, pls. 1-4.

Westcott, C. 1964. *The Gardner's Bug Book*, 3rd edn. Garden City, N.Y.: Doubleday and Company.

West-Eberhard, M.J. 1983. *Polistes* (quita calzon, lengua de vaca [name of nest], paper wasp). IN: Janzen, D.H., (Ed.), *Costa Rican Natural History*, pp. 758-760. Chicago: University of Chicago Press.

Westfall, M.J., Jr. 1984. Odonata. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 126-176. Dubuque: Kendall/Hunt Publishing Co.

Westwood, J.O. 1854. Contributions to fossil entomology. *Quart. J. Geol. Soc. London*, 10: 378-396.

Weyenbergh, H. 1869. Sur les insectes fossiles eu calcaire lithographique de la Bavière. *Arch. Mus. Teyler*, (2), 2: 247-294.

Weygoldt, P. 1979. Significance of later embryonic stages and head development in arthropod phylogeny. IN: Gupta, A.P., (Ed.), *Arthropod Phylogeny*, pp. 107-135. New York: Van Nostrand Reinhold Co.

Whalley, P.E.S. 1971. The Thyrididae (Lepidoptera) of Africa and its islands: A taxonomic and zoogeographic study. *Bull. Brit. Mus. Nat. Hist. (Entomol.), Suppl.*, 17: 1-198, pls. 1-68.

Whalley, P.E.S. 1977. Lower Cretaceous Lepidoptera. *Nature*, 266: 526.

Whalley, P.E.S. 1978. New taxa of fossil and recent Micropterygidae with a discussion of their evolution and a comment on the evolution of the Lepidoptera (Insecta). *Ann. Transv. Mus.*, 31: 71-86.

Whalley, P.E.S. 1983. A survey of Recent and fossil cicadas (Insecta, Hemiptera-Homoptera) in Britain. *Bull. Brit. Mus. Nat. Hist., Geol.*, 37: 139-147.

Whalley, P.E.S. 1985. The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. *Bull. Brit. Mus. Nat. Hist., Geol. Ser.*, 39: 107-189.

Whalley, P.E.S. 1986. A review of the current fossil evidence of Lepidoptera in the Mesozoic. *Biol. J. Linn. Soc.*, 28: 253-271.

Whalley, P.E.S. 1988. Mesozoic Neuroptera and Raphidioptera (Insecta) in Britain. *Bull. Brit. Mus. Nat. Hist., Geol. Ser.*, 44: 45-63.

Whalley, P.E.S. and Jarzembowski, E.A. 1981. A new assessment of *Rhyniella*, the earliest known insect, from the Devonian of Rhynie, Scotland. *Nature*, 291: 317.

Whalley, P.E.S. and Jarzembowski, E.A. 1985. Fossil insects from the lithographic limestone of Montsech (Late Jurassic-Early Cretaceous), Lérida Province, Spain. *Bull. Brit. Mus. Nat. Hist., Geol. Ser.*, 38: 381-412.

Whedon, A.D. 1927. The structure and transformation of the labium of *Anax junius*. *Biol. Bull.*, 53: 286-301.

Wheeler, Q.D. 1984. Associations of beetles with slime molds: ecological patterns in the Anisotomini (Leiodidae). *Bull. Entomol. Soc. Am.*, 30: 14-18.

Wheeler, Q.D. 1986. Rediscovery and cladistic placement of the genus *Cainosternum* (Coleoptera: Leiodidae). *Ann. Entomol. Soc. Am.*, 79: 377-383.

Wheeler, Q.D. and Blackwell, M., (Eds.). 1984. *Fungus-Insect Relationships: Perspectives in Ecology and Evolution*. New York: Columbia University Press. 663 p.

Wheeler, W.M. 1910. *Ants: Their Structure, Development and Behavior*. New York: Columbia University Press. 663 pp.

Wheeler, W.M. 1914. The ants of the Baltic amber. *Schrift. Okon. Ges. Köningsberg*, 55: 1-142.

Wheeler, W.M. 1927. The physiognomy of insects. *Quart. Rev. Biol.*, 2: 1-36.

White, D.S., Brigham, W.U. and Doyen, J.T. 1984. Aquatic Coleoptera. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 361-437. Dubuque: Kendall/Hunt Publishing Co.

White, J. and Strehl, C.E. 1978. Xylem feeding by periodical cicada nymphs on tree roots. *Ecol. Entomol.*, 3: 323-327.

White, R.E. 1983. *A Field Guide to the Beetles of North America.* Boston: Houghton Mifflin Co. 368 p.

Whitfield, F.G.S. 1925. The relation between the feeding habits and the structure of the mouth-parts in the Asilidae (Diptera). *Proc. Zool. Soc.*, 1925: 599-638.

Whiting, J.H., Jr., Black, H.L. and Jorgensen, C.D. 1989. A scanning electron microscopy study of the mouthparts of *Paraponera clavata* (Hymenoptera: Formicidae). *Pan-Pac. Entomol.*, 65: 302-309.

Wichard, W. 1983. Köcherfliegen des Dominikanischen Bernsteins. III. *Chimarra succini* n.sp. (Stuttgarter Bernsteinsammlung: Trichoptera, Philopotamidae). *Stutt. Beit. Naturk.*, (B), 95: 1-8.

Wichard, W. 1987. Caribbean amber caddisflies--biogeographical aspects. *Proc. Fifth Int. Symp. Trichoptera*, pp. 67-69.

Wickham, H.F. 1913. Fossil Coleoptera from Florissant in the United States National Museum. *Proc. U.S. Natl. Mus.*, 45: 283-303.

Wickham, H.F. 1914. New Miocene Coleoptera from Florissant. *Bull. Mus. Comp. Zool.*, 58: 423-493.

Wickham, H.F. 1929. Coleoptera from the Lower Eocene (Wilcox) clays. *J. Washington Acad. Sci.*, 19: 148-150.

Wieland, G.R. 1925. Rhaetic crane flies from South America. *Am. J. Sci.*, 9: 21-28.

Wiesenborn, W.D. and Morse,J.G. 1988. The mandible and maxillary stylets of *Scirtothrips citri* (Moulton) (Thysanoptera: Thripidae). *Pan-Pac. Entomol.*, 64: 39-42.

Wiggins, G.B. 1959. A new family of Trichoptera from Asia. *Can. Entomol.*, 91: 745-757.

Wiggins, G.B. 1960. The unusual pupal mandibles in the caddis-fly family Phryganeidae (Trichoptera). *Can. Entomol.*, **92**: 449-457.

Wiggins, G.B. 1977. *Larvae of the North American Caddisfly Genera (Trichoptera).* Toronto: University of Toronto Press. 401 p.

Wiggins, G.B. 1982. Trichoptera. IN: Parker, S.P., (Ed.), *Synopsis and Classification of Living Organisms*, 2: 599-612. New York: McGraw-Hill Book Co.

Wiggins, G.B. 1984. Trichoptera. IN: Merritt, R.W. and Cummins, K.W., (Eds.), *An Introduction to the Aquatic Insects of North America*, 2nd edn., pp. 271-311. Dubuque: Kendall/Hunt Publishing Co.

Wigglesworth, V.B. 1964. The dietary of insects. IN: Wigglesworth, V.B., *The Life of Insects*, pp. 50-75. Cleveland: World Publishing Co.

Wilcox, J. 1981. Mydidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, **27**: 533-540.

Wilcox, J. and Baker, W.W. 1935. The deciduous cusps of the Alophini (Coleoptera-Curculionidae). *Bull. Brooklyn Entomol. Soc.*, **30**: 20-21, pl. 1.

Wilczek, M. 1967. The distribution and neuroanatomy of the labellar sense organs of the blowfly *Phormia regina* Meigen. *J. Morphol.*, **122**: 175-201.

Wille, A. 1959. A new fossil stingless bee (Melponini) from the amber of Chiapas, Mexico. *J. Paleontol.*, **33**: 849-852.

Wille, A. 1977. A general review of the fossil stingless bees. *Rev. Biol. Trop.*, **25**: 43-46.

Wille, A. and Chandler, L.C. 1964. A new stingless bee from the Tertiary amber of the Dominican Republic (Hymenoptera: Meliponini). *Rev. Biol. Trop.*, **12**: 187-195.

Wille, J. 1922. Biologische und physiologische Beobachtungen und Versuche an der Kasefliegenlarve (*Piophila casei* L.). *Zool. Jb. (Allg., Zool., Physiol.)*, **39**: 301-320.

Willem, V. 1924. Observations sur "*Machilis maritima*." *Bull. Biol. France Belg.*, **58**: 306-320.

Willemstein, S.C. 1980. Pollen in Tertiary insects. *Acta Bot. Neerland.*, **29**: 57-58.

Willemstein, S.C. 1987. An evolutionary basis for pollination ecology. *Leiden Bot. Ser.*, 10: 1-425.

Williams, F.X. 1913. The Larridae of Kansas. *Kansas Univ. Sci. Bull.*, 8: 121-213, pls. 22-30.

Williams, I.W. 1933. The external morphology of the primitive tanyderid dipteron *Protoplasa fitchi* O.S., with notes on the other Tanyderidae. *J. New York. Entomol. Soc.*, 41: 1-34, pls. 1-7.

Williams, I.W. 1938. The comparative morphology of the mouth-parts of the order Coleoptera treated from the standpoint of phylogeny. *J. New Entomol. Soc.*, 46: 245-289.

Williams, J.A. and Edman, J.D. 1968. Occurrence of blood meals in two species of *Corethella* in Florida. *Ann. Entomol. Soc. Am.*, 61: 1336.

Williams, L.H. 1954. The feeding habits and food preferences of Acrididae and the factors which determine them. *Trans. Roy. Entomol. Soc. London*, 105: 423-454.

Willis, D.M. 1949. The anatomy and histology of the head, gut and associated structures of *Typhlocyba ulmi*. *Proc. Zool. Soc. London*, 118: 984-1001.

Williston, S.W. 1908. *Manual of North American Diptera*, 3rd edn. New Haven: James Hathaway. 405 p.

Willmann, R. 1983. Widerspruchliche Rekonstruktionen der Phylogenese am Biespiel der ordnung Mecoptera (Schnabelfliegen; Holometabola). *Paläont. Z.*, 57: 285-308.

Willmann, R. 1987. The phylogenetic system of the Mecoptera. *Syst. Entomol.*, 12: 519-524.

Wilson, E.O. 1971. *The Insect Societies*. Cambridge, MA: Harvard University Press. 548 p.

Wilson, E.O., Carpenter, F.M. and Brown, W.L., Jr. 1967a. The first Mesozoic ants. *Science*, 157: 1038-1040.

Wilson, E.O., Carpenter, F.M. and Brown, W.L., Jr. 1967b. The first Mesozoic ants, with the description of a new subfamily. *Psyche*, 74: 1-19, pls. 1-3.

Wilson, E.O. and Holldobler, B.K. 1990. *The Ants*. Cambridge, MA: Harvard University Press.

Wilson, M.V.H. 1978a. Paleogene insect faunas of western North America. *Quaest. Entomol.*, 14: 13-34.

Wilson, M.V.H. 1978b. Evolutionary significance of North American Paleogene insect faunas. *Quaest. Entomol.*, 14: 35-42.

Wilson, M.V.H. 1983. Is there a characteristic rate of radiation for the insects? *Paleobiology*, 9: 79-85.

Wink, M., Hartmann, T., Witte, L. and Rheinheimer, J. 1982. Interrelationship between quinolizine alkaloid-producing legumes and infesting insects: exploitation of the alkaloid-containing phloem sap of *Cytisus scoparius* by the broom aphid *Aphis cytisorum*. *Z. Naturfor.*, 37: 1081-1086.

Winkler, D. 1959. Die Muskulatur der Larve von *Limnophilus flavicornis* Fabr. (Trichopt., Limnophilidae). *Deut. Entomol. Z.*, N.S., 6: 112-128.

Winston, M.L. 1979. The proboscis of the long-tongued bees: a comparative study. *Univ. Kansas Sci. Bull.*, 51(22): 631-667.

Winston, M.L. and Michener, C.D. 1977. Dual origin of highly social behavior among bees. *Proc. Natl. Acad. Sci. USA*, 74: 1135-1137.

Wirth, W.W. 1952. Three new Nearctic species of *Systenus* with a description of the immature stages from tree cavities. *Proc. Entomol. Soc. Washington*, 54: 236-244.

Wirth, W.W. and Stone, A. 1956. Aquatic Diptera. IN: Usinger, R.L., (Ed.), *Aquatic Insects of California, with Keys to North American Genera and California Species*, pp. 372-482. Berkeley: University of California Press.

Wirtz, H.-P. 1985. Eindringungsweise der Mundwerkzeuge von Kreibelmucken durch eine Membran (Diptera: Simuliidae). *Entomol. Gen.*, 10: 133-138.

Wirtz, H.-P. 1987a. Eindringen der Mundwerkzeuge von Raubwanzen durch eine Membran (Hemiptera: Reduviidae). *Entomol. Gen.*, 12: 147-153.

Wirtz, H.-P. 1987b. Eindringen der Mundwerkzeuge von Gnitzen durch eine künstliche Membran (Diptera: Ceratopogonidae). *Zool. Jb. (Anat.)*, 116: 317-322.

Withycombe, C.L. 1922. Notes on the biology of some British Neuroptera (Planipennia). *Trans. Entomol. Soc. London*, 1922: 501-594

Withycombe, C.L. 1923. Systematic notes on the Crocini (Nemopteridae), with descriptions of new genera and species. *Trans. Entomol. Soc. London*, 1923: 269-287.

Withycombe, C.L. 1924. Some aspects of the biology and morphology of the Neuroptera. With special reference to the immature stages and their possible phylogenetic significance. *Trans. Entomol. Soc. London*, 1924: 303-406.

Wittmer, W. 1963. A new cantharid from the Chiapas amber of Mexico. *Univ. Calif. Publ. Entomol.*, 31: 53.

Witzke, G. 1973. Beziehungen zwischen den Mundgliedmassen der Imago von *Pterostichus niger* (Col., Carabidae) und ihrer karnivoren Lebensweise. *Entomol. Z.*, 83: 185-190.

Woke, P.A. 1941. Structure and development of the alimentary canal of the southern armyworm larva. *U.S. Dept. Agr. Tech. Bull.*, 762: 1-27.

Wolberg, D.L., West, S., Hall, J.P. and Zidek, J. 1988. Probable caddisfly (Trichoptera: Insecta) larval cases from the Fruitland Formation (Campanian-Maastrichtian) of the Fossil Forest, San Juan County, New Mexico. *Bull. New Mexico Bur. Mines Min. Resour.*, 122: 29-31.

Wollman, E. 1911. Sur l'elevage des mouches steriles. Contribution a la conaissance du role des microbes dans les voies digestives. *Ann. Inst. Pasteur*, 25: 79-88.

Wolter, H. 1963. Vergleichende Untersuchungen zur Anatomie und Funktionsmorphologie der Stechend-saugenden Mundwerkzeuge der Collembolen. *Zool. Jb. (Anat.)*, 81: 27-100.

Wong, H.R. 1963. The external morphology of the adults and ultimate larval instar of the larch sawfly, *Pristiphora erichsonii* (Htg.) (Hymenoptera: Tenthredinidae). *Can. Entomol.*, 95: 897-921.

Wood, D.M. 1981a. Axymyiidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera." Vol. 1. *Res. Branch Agr. Canada*, 27: 209-212.

Wood, D.M. 1981b. Pachyneuridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera." Vol. 1. *Res. Branch Agr. Can.*, 27: 213-216.

Wood, G.C. 1981c. Asilidae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera," vol. 1. *Res. Branch Agr. Canada*, 27: 549-574.

Wood, D.M. 1987. Oestridae. IN: McAlpine, J.F., et al., (Eds.), "Manual of Nearctic Diptera." Vol. 1. *Res. Branch Agr. Canada*, **28**: 1147-1158.

Wood, D.M. and Borkent, A. 1989. Phylogeny and classification of the Nematocera. IN: Alpine, J.F. and Wood, D.M., (Eds.), "Manual of Nearctic Diptera," vol. 3. *Res. Branch Agr. Canada*, 32: 1333-1370.

Woodley, N.E. 1989. Phylogeny and classification of the "orthorrhaphous" Brachycera. IN: McAlpine, J.F. and Wood, D.M., (Eds.), "Manual of Nearctic Diptera," vol. 3. *Res. Branch Agr. Canada*, 32: 1371-1396.

Wootton, A. 1984. *Insects of the World*. New York: Facts on File Publications. 224 p.

Wootton, R.J. 1972. The evolution of insects in fresh water ecosystems. IN: Clark, R.B. and Wootton, R.J., (Eds.), *Essays in Hydrobiology*, pp. 69-82. Exeter: University of Exeter Press.

Wootton, R.J. 1981. Palaeozoic insects. *Ann. Rev. Entomol.*, **26**: 319-344.

Wootton, R.J. 1986. Palaeontology and phylogeny. IN: Betts, C., Laffoley, D.A. and Cribb, P.W., (Eds.), *The Hymenopterist's Handbook*, pp. 1-7. Hanworth, Great Britain: The Amateur Entomologist's Society.

Wootton, R.J. 1988. The historical ecology of aquatic insects: an overview. *Palaeogeog., Palaeoclim., Palaeoecol.*, **62**: 477-492.

Wundt, H. 1961. Der Kopf der Larve von *Osmylus chrysops* L. (Neuroptera, Planipennia). *Zool. Jb. (Anat.)*, **79**: 557-662.

Wyatt, R. 1983. Pollinator-plant interactions and the evolution of breeding systems. IN: Real, L., (Ed.), *Pollination Biology*, pp. 51-95. New York: Academic Press.

Wygodzinsky, P. 1944. Contribuiçao al conhecimento da familia Machilidae (Thysanura) do Mèxico, do Brasil e da Argentina. *Rev. Entomol.*, **15**: 54-96.

Wygodzinsky, P. 1945. Contribuiçāo ao conhecimento dos "Entotrophi" e "Thysanura" de Portugal. II. Familia "Machilidae" (Thysanura). *Rev. Bras. Biol.*, **5**: 69-80.

Wygodzinsky, P. 1948. Redescription of *Nesomachilis maoricus* Tillyard, 1924, with notes on the family "Machilidae" (Thysanura). *Dom. Mus. Rec. Entomol.*, **1**: 69-78.

Wygodzinsky, P. 1961. On a surviving representative of the Lepidotrichidae (Thysanura). *Ann. Entomol. Soc. Am.*, 54: 621-627.

Wygodzinsky, P. 1971. A note on a fossil machilid (Microcoryphia) from the amber of Chiapas, Mexico. *Univ. California Publ. Entomol.*, 63: 101-102.

Wygodzinsky, P. and Schmidt, K. 1980. Survey of the Microcoryphia (Insecta) of the northeastern United States and adjacent provinces of Canada. *Am. Mus. Novit.*, 2701: 1-17.

Yablokov-Kinzorian, S.M. 1962. Some *Sternoxia* (Coleoptera) from Baltic amber. *Paleontol. Zhur.*, 1962: 81-89. [In Russian.]

Yasuda, T. 1962. On the larva and pupa of *Neomicropteryx nipponensis* Issiki, with its biological notes. *Kontyu*, 30: 130-136.

Yoshimoto, C.M. 1964. Insects of Campbell Island. Hymenoptera: Diapriidae. *Pac. Insects Mon.*, 7: 507-508.

Yoshimoto, C.M. 1975. Cretaceous chalcidoid fossils from Canadian amber. *Can. Entomol.*, 107: 499-528.

Yoshimoto, C.M. 1984. *The Insects and Arachnids of Canada. Part 12. The Families and Subfamilies of Canadian Chalcidoid Wasps (Hymenoptera: Chalcidoidea).* Ottawa: Canadian Government Publishing Centre. 149 p.

Young, A.M. 1984. On the evolution of cicada x host-tree associations in Central America. *Acta Biotheorr.*, 33: 163-198.

Young, J.H. 1953. Embryology of the mouthparts of the Anoplura. *Microentomology*, 18: 85-133.

Yuasa, H. 1920. The anatomy of the head and mouth-parts of Orthoptera and Euplexoptera. *J. Morphol.*, 33: 251-307.

Yuasa, H. 1922. A classification of the larvae of the Tenthredinoidea. *Illinois Biol. Mon.*, 7: 1-172.

Yumoto, T. 1986. The ecological pollination syndromes of insect-pollinated plants in alpine meadow. *Ecol. Res.*, 1: 83-95.

Yumoto, T. 1987. Pollination systems in a warm temperate evergreen broad-leaved forest on Yaku Island. *Ecol. Res.*, 2: 133-145.

Yumoto, T. 1988. Pollination systems in the cool temperate mixed coniferous and broad-leaved forest zone of Yakushima Island. *Ecol. Res.*, 3: 117-129.

Zaitland, L.M. and Larsen, J.R. 1984. Morphology of the head of *Mydas clavatus* Drury (Diptera, Mydaidae). *Int. J. Insect Morphol. Embryol.*, 13: 105-136.

Zaitzev, V.F. 1981. Vergleich der Tertiären (Oligozän und Miozän) und Rezenten Bombyliidenfauna Europas (Diptera, Bombyliidae). *Acta Entomol. Jugosl.*, 17: 103-106.

Zaitzev, V.F. 1982. Microstructure of the labella of the fly proboscis. 1. Structure of the apparatus closing the pseudotracheae. *Entomol. Rev.*, 61: 60-69.

Zaka-ur-Rab, M. 1963. Musculature of the sucking pump of *Argina cribaria* Clerck (Lepidoptera: Hypsidae). *Beit. Entomol.*, 13: 654-657.

Zaka-ur-Rab, M. 1978. Morphology of the head of *Bathyaulax alami* Zaka (Hymenoptera: Braconidae). *Zool. Jb. (Anat.)*, 99: 421-436.

Zalessky, G. 1937. Ancestors of some groups of the present day insects. *Nature*, 140: 847-848.

Zalessky, G. 1955. On two new Permian dragonflies of the order Protodonata. *Dokl. Acad. Nauk USSR*, 104: 630-633.

Zessin, W. 1987. Variabilität, Merkmalswandel und Phylogenie der Elcanidae im Jungpaläozoikum und Mesozoikum und die Phylogenie der Ensifera (Orthopteroidea, Ensifera). *Deut. Entomol. Z.*, N.F., 34: 1-76, pls 1-2.

Zeuner, F.E. 1927. Eine Sphingidenraukpe aus dem Obermiozän von Böttingen. *Paläont. Z.*, 8: 321-326.

Zeuner, F.E. 1929. Die Insekten des tertiären Sprudelsinters von Böttingen (Schwabische Alb). *Paläont. Z.*, 11: 330-339.

Zeuner, F.E. 1931. Die Insektenfauna des Böttinger Marmors. *Fortsch. Geol. Paleontol.*, 9: 247-406, pls. 1-19.

Zeuner, F.E. 1936. The Recent and fossil Tympanophorinae (Tettigoniidae, Saltatoria). *Trans. Entomol. Soc. Canada*, 85: 287-302.

Zeuner, F.E. 1937. Descriptions of new genera and species of fossil Saltatoria (Orthoptera). *Proc. Roy. Entomol. Soc. London*, (B), 6: 154-159.

Zeuner, F.E. 1938. Die Insektenfauna des Mainzer Hydrobienkalks. *Paläont. Z.*, 20: 104-159, pls. 13-17.

Zeuner, F.E. 1939. *Fossil Orthoptera Ensifera.* London: British Museum of Natural History. 320 p., 80 pls.

Zeuner, F.E. 1942. The Locustopsidae and the phylogeny of the Acridoidea (Orthoptera). *Proc. Roy. Entomol. Soc. London*, (B), 11: 1-18.

Zeuner, F.E. 1961. A Triassic insect fauna from the Molteno Beds of South Africa. *Trans. 11th Int. Congr. Entomol.*, 1: 304-306.

Zeuner, F.E. 1962. Fossil insects from the Lower Lias of Charmouth, Dorset. *Bull. Brit. Mus. Nat. Hist., Geol.*, 7: 153-171, pls. 24-27.

Zeuner, F.E., Manning, F.J. and Morris, S.F. 1976. A monograph of fossil bees (Hymenoptera: Apoidea). *Bull. Brit. Mus. (Nat. Hist.), Geol.*, 27: 149-268.

Zeve, V.H. and Howell, D.E. 1962. The comparative external morphology of *Trichobius corynorhini*, *T. major*, and *T. sphaeronotus* (Diptera, Streblidae). Part 1. The head. *Ann. Entomol. Soc. Am.*, 55: 685-694.

Zhavoronkova, T.N. 1969. Certain structural peculiarities of the Carabidae (Coleoptera) in relation to their feeding habits. *Entomol. Rev.*, 48: 462-471.

Zherikin, V.V. 1968. A new find of Curculionoidea from Baltic amber. *Bull. Moscow Soc. Nat. Geol.*, 43: 156. [In Russian.]

Zherikin, V.V. 1977. Attelabidae, Curculionidae. IN: Arnoldi, L.V., Zherikin, V.V., Nitriken, L.M. and Ponomarenko, A.G., Mesozoic Coleoptera. *Trans. Paleontol. Inst.*, 161: 176-182.

Zherikin, V.V. 1978. Development and change in the Cretaceous and Cenozoic insect fauna complex. *Trans. Paleontol. Inst.*, 165: 1-198. Moscow: Academy of Sciences. [In Russian.]

Zherikin, V.V. and Sukacheva, I.D. 1973. On Cretaceous insect-bearing amber (retinite) from northern Siberia. IN: Bei-Benko, G.Y., (Ed.), *Dokl. 24th Ann. Lect. Memory N.A. Kholodkovskogo*, 24: 3-48. Moscow: Academy of Sciences. [In Russian.]

Zia, Y. 1934. Etude morphologique et systematique des Languriidae de Tonkin. *Mem. Fac. Sci., Univ. Paris*, 554: 1-41.

Zimmerman, E.C. 1948. Homoptera: Sternorhyncha. *Ins. Hawaii*, 5: 1-464.

Zimmermann, E.C. 1971. Mexican Miocene amber weevils (Insecta: Coleoptera: Curculionoidea). *Univ. California Publ. Entomol.*, 63: 103-106.

Zimmerman, E.C. 1978. Microlepidoptera. Part II. Gelechioidea. *Ins. Hawaii*, 9: 883-1903.

Zolessi, L.C. de 1968. Morphologie, endosquelette et musculature d'un acridien aptère (Orthoptera: Proscopiidae). *Trans. Roy. Entomol. Soc. London*, 120: 55-113.

Zur Strassen, R. 1973. Insektenfossilien aus der unteren Kreide--5: Fossile Fransenflüger aus Mesozoichem Bernstein des Libanon (Insecta: Thysanoptera). *Stutt. Beitr. Naturk.*, (A), 256: 1-51.

Zwick, P. 1967. Beschreibung der aquatischen Larve von *Neurorthus fallax* (Rambur) und Errichtung der neuen Plannipennien-Familie Neurorthidae fam. nov. *Gewass. Abwass.*, 44/45: 65-86.

Zwick, P. 1980. Plecoptera (Sternfliegen). IN: Beier, M., (Ed.), *Handbuch der Zoologie*, Band 4, Teil 2, Lfg. 26: 1-115. Berlin: Walter de Gruyter.

THE UNIVERSITY OF CHICAGO

USE OF A PHENETIC ANALYSIS OF RECENT HEXAPOD MOUTHPARTS FOR THE DISTRIBUTION OF HEXAPOD FOOD RESOURCE GUILDS IN THE FOSSIL RECORD

VOLUME FIVE

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE PHYSICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
DEPARTMENT OF GEOPHYSICAL SCIENCES

BY
CONRAD CHRISTOPHER LABANDEIRA

CHICAGO, ILLINOIS
AUGUST, 1990

APPENDIX A

CHARACTER-STATES FOR INSECT MOUTHPART AND HEAD CHARACTERIZATION

In hierarchical order, character-groups are capitalized, boldfaced and in Roman numerals; characters are numbered and in boldfaced type; and character-states are lettered and in lower-case type.

STRUCTURAL DATA

I. HEAD AND GENERAL MOUTHPART-RELATED STRUCTURES [GROUP I]

1. **Head Shape** (three-dimensional; from occiput base to rostrum tip, including projecting mouthparts).
   - A. Head inconspicuous and marginally projecting; partly retracted into thorax.
   - B. Head transversely-elongated (e.g. Odonata, Strepsiptera, Lepidoptera).
   - C. Head quadrate or spheroidal (e.g. Blattodea, Orthoptera).
   - D. Head anteriorly prolonged; porrect (e.g. Reduviidae, Hydrometridae).
   - E. Head vertically prolonged (e.g. *Tryxalis*).
2. **Rostrum or proboscis development** (projection of head or mouthparts beyond an epistomal suture).
   - A. Absent.
   - B. Rostrum or proboscis short (length less than two times the greatest width).
   - C. Rostrum or proboscis long (length between two and eight times the greatest width).
   - D. Rostrum or proboscis very long (length greater than eight times the greatest width).
3. **Genal region or malar space**, including the maxillary plate or paraclypeal lobe.
   - A. Gena absent, inconspicuous, or undiagnostic in blind adult species.
   - B. Gena prominent or well-developed.
   - C. Gena moderately to minimally developed.
   - D. Gena expansive; considerable separation of eyes from mouthparts and convergent coronally.
   - E. Gena expanded dorsoventrally, surrounding the ocelli; forming most of the cranium (Holometabola).
   - F. Gena pronounced; part of a cephalopharyngeal capsule.
4. **Gula or hypostome** (also postgenae or malar space); separation of foramen magnum from labium.
   - A. Gula absent or inconspicuous.
   - B. Gula prominent or well-developed.
   - C. Gula moderately to minimally developed.
   - D. Gula elongated into a pregula surrounded by a pregena, or prolonged anteriorly (postgena).
   - E. Gular region not delimited by sutures; part of a cephalopharyngeal capsule.
5. **Lorum, or mandibular plate.**
   - A. Lorum absent or inconspicuous.
   - B. Lorum prominent or well-developed.
   - C. Lorum moderately developed.
6. **Frontal and vertical region.**
   - A. A coronal suture merging anteriorly with a clypeal or frontoclypeal suture.
   - B. Wide and triangular, delimited by an inverted Y-shaped epistomal suture; clypeofrontal fusion.
   - C. Frontal/vertical region anteriorly prolonged beyond eyes.
   - D. Frontal/vertical region obscure; part of a cephalopharyngeal capsule or covered by tissue.
   - E. Frontal/vertical region incised or cleft (calyptrate Diptera; adult Lepidoptera).
7. **Head protractability/retractability.**
   - A. Head not protractable.
   - B. Head protractable.

8. **Feeding-related modifications indirectly associated with the head (excluding mouthparts).**
   A. Modifications absent.
   B. Raptorial or grasping prothoracic legs (e.g. Mantidae, Odonata, Nepidae, Mantispidae).
   C. Anterior prolongation of the prothorax enveloping the posterior part of the head.
   D. Presence of forcipate cerci for food capture (Entotrophi, Dermaptera).
   E. Prothoracic legs antenna-like and/or tactile (Protura).
   F. Head joined to thorax, forming a cephalothorax (or cephalotheca in pupae).
   G. Presence of backward-directed ctenidia (genal combs) or spines on head margin.
   H. Presence of pharyngeal or esophageal filtering organs.
   I. Presence of rows of filtering setae on forelegs.

II. SENSE ORGANS OF THE HEAD [GROUP II]

9. **Antennae.**
   A. Antennae absent or vestigial.
   B. Antennae setaceous.
   C. Antennae filiform.
   D. Antennae moniliform.
   E. Antennae pectinate, plumose, or brush-like.
   F. Antennae serrate.
   G. Antennae clavate.
   H. Antennae capitate.
   I. Antennae geniculate.
   J. Antennae lamellate or flabellate.
   K. Antennae stylate.
   L. Antennae aristate.
   M. Antennae very short and stubby; papillate (e.g. Lepidoptera larvae).
   N. Antennae setigerous (*Psychoda* larva).
   O. Antennae palpiform (larval Coleoptera).
   P. Antennae spathulate or some modification thereof.
10. **Ocelli, pseudocelli, or stemmata.**
   A. Absent.
   B. One in number.
   C. Two in number.
   D. Three in number.
   E. More than three in number.
11. **Compound Eyes.**
   A. Absent or vestigial (e.g. Protura, some Gryllidae and Coleoptera).
   B. Expansive, not stalked, and often holoptic (e.g. Odonata, Homoptera).
   C. Stalked (e.g. male Baetidae, Diopsidae).
   D. Moderately developed and dichoptic (e.g. Dermaptera, Mantodea) to dimunitive (e.g. Collembola).
   E. Divided into separate units (e.g. Gyrinidae, Trialeuridae, adult male Coccidae).

III. GENERAL FEATURES OF MOUTHPART APPARATI [GROUP III]

12. **Mouthpart placement on the head capsule.**
   A. Agnathous.
   B. Prognathous; facial aspect directed forward and mouthparts directed forward.
   C. Hypognathous; facial aspect directed forward and mouthparts directed downward.
   D. Opisthognathous-auchenorrhynchous; mouthparts projecting from below the neck.
   E. Opisthognathous-sternorrhynchous; mouthparts under the venter of the head and thorax.
   F. Entognathous.

13. **Mouthpart basic type.**
    A. Mandibulate.
    B. Stylate-nonhaustellate (e.g. Protura, *Haematomyzus*, Cerylonidae).
    C. Stylate-haustellate (e.g. Heteroptera, nematocerous Diptera).
    D. Glossate (e.g. Hymenoptera).
    E. Siphonate (e.g. higher Lepidoptera, *Nemognatha*).
    F. Labellate (e.g. Trichoptera, cyclorrhaphous Diptera).
    G. Nontrophic or passive food assimilation (e.g. adult Ephemeroptera; Strepsiptera).
    H. Mandibulo-suctorial (e.g. larval Planipennia, Cantharidae).
14. **Mouthpart stylet number.**
    A. Stylets absent.
    B. Stylets one.
    C. Stylets two.
    D. Stylets three.
    E. Stylets four.
    F. Stylets six.
    G. Stylets nine.
    H. Stylets greater than nine; numerous, small denticles.
15. **Mouthpart symmetry.**
    A. Multielement asymmetry.
    B. Symmetrical.
    C. Single element asymmetry only (mostly mandibles).
16. **Food pump.**
    A. Absent.
    B. Clypeal or cibarial (preoral and dilatory; e.g. Homoptera).
    C. Pharyngeal (dilatory; e.g. some Protura, Collembola, larval Lepidoptera).
    D. Esophageal (postoral and dilatory; e.g. some Protura).
    E. Labral and clypeal (preoral and dilatory, e.g. Mecoptera).
    F. Clypeal and pharyngeal.
17. **Protractability/retractability of major food-reaching mouthpart elements.**
    A. Absent.
    B. Present (e.g. Heteroptera, some Diptera, Lepidoptera).

IV. CLYPEAL REGION [GROUP IV]

18. **Shape of entire clypeal complex**, parallel to sagittal plane, below the frons, and above the labrum.
    A. Clypeus absent, vestigial, or indistinguishably fused with frontal region.
    B. Clypeus vertically elongate; length/width less than 0.5.
    C. Clypeus quadrate or nearly so; length/width between 0.5 and 2.0.
    D. Clypeus transversely elongate; length/width greater than 2.0.
19. **Clypeal subsegmentation.**
    A. Clypeus absent or vestigial.
    B. Clypeus divided into one segment only.
    C. Clypeus divided into two segments: an anteclypeus + postclypeus or a preclypeus + postclypeus.
    D. Clypeus fused to the labrum (clypeolabrum).
    E. Clypeus fused to the frons (frontoclypeus).

V. LABRAL REGION [GROUP V]

20. **Shape of the labral main body,** with respect to the sagittal plane (excluding tormae).
    A. Labrum absent or vestigial.
    B. Labrum transversely elongate; length/width greater than 0.5.
    C. Labrum quadrate, trapezoidal or broadly triangular; length/width between 0.50 and 2.0.
    D. Labrum vertically elongate; length/width greater than 2.0 and less than 4.0.
    E. Labrum vertically very elongate; length/width greater than 4.0.
21. **Labral subsegmentation.**
    A. Labrum absent or vestigial.
    B. Labrum consisting of one segment only (e.g. neolabrum).
    C. Labrum divided into two segments (e.g. neolabrum + archilabrum, or neolabrum + prelabrum).
    D. Labrum a nasale.
    E. Labrum part of a clypeolabrum.
22. **Modification of the distal labral margin.**
    A. Labrum absent or vestigial.
    B. Margin straight to shallowly curvilinear, a ventral convex or concave margin.
    C. Margin notched or otherwise divided medially.
    D. Margin mucronate and acuminate.
    E. Margin broadly triangular and acute.
    F. Margin spatulate or lingulate process.
    G. Margin pectinate (coarse setae or bristles; often a comb).
    H. Margin a beak or stylet brace or guide fused to a postlabral epipharyngeal process.
    I. Margin spinose.
    J. Margin membranous.
    K. Margin aperturate (labral cone or cup).
    L. Margin piliferate.
    M. Margin undulatate to serrate.
    N. Margin a penicillate (brush).
23. **Labral participation in a multielement mouthpart structure.**
    A. Multielement co-optation absent.
    B. Labrum part of a segmented haustellum, forming a brace.
    C. Labrum part of a mouthcone, buccal cone, or labral cup (e.g. Thysanoptera, some Coleoptera).
    D. Labrum part of a rostrum.
    E. Labrum-epipharynx part of a fasiculate or modified fasiculate haustellum.
    F. Labrum is or is part of a labellum.
    G. Labrum is a stylus or stylet-like.
    H. Labrum is a holding device for a labial mask (e.g. larval Odonata).
    I. Labrum is a guide for stylet movement.
    J. Labrum participating in a glossate proboscis.
    K. Labrum-epipharynx comprising a siphon (*Eristalis* larvae).
    L. Labrum is a support for a maxillary siphon (adult Lepidoptera).
    M. Labrum part of a silk-producing apparatus (larval Lepidoptera).

VI. PHARYNGEAL REGION [GROUP VI]

24. **Food ingestion region size.**
    A. Diminutive; an enclosed canal with active suction.
    B. Intermediate; a pseudotracheal system with capillary action.
    C. Enlarged; a pharyngeal/esophageal system.
    D. Food ingestion region absent.

25. **Hypopharynx type.**
   A. Hypopharynx absent or vestigial.
   B. Hypopharynx lingulate to spatulate, a single lobe (e.g. Odonata, Blattodea, Orthoptera).
   C. Hypopharynx bilobed, or with two lateral superlingulae or bars.
   D. Hypopharynx trilobed, with a lingua (=tongue) and two lateral superlingulae (=maxillulae).
   E. Hypopharynx triangular and hood-like, and acutely or acuminately tapering (e.g. some Thysanura).
   F. Hypopharynx pectinate, with 1 or 2 rows of pectinate setae or teeth on superlingulae.
   G. Hypopharynx long and stylate, with a salivary syringe (e.g. Asilidae, Anoplura, Thysanoptera).
   H. Hypopharynx with a region of dense hair or bristles ("brush"), or a fimbrate tongue.
   I. Hypopharynx a labellate haustellum anteriorly; with a salivary duct.
   J. Hypopharynx adjoined to the labrum or labium as an inconspicuous lobe.
   K. Hypopharynx a bilobed structure of lateral brushes or teeth; associated with a labial spinneret.
   L. Hypopharynx with superlingulae, two lateral ovoidal sclerites, and a medial basal sitophore.
   M. Hypopharynx a broad, H-shaped ramus, articulating with mandibles and cephalopharyngeal skeleton.
   N. Hypopharynx a salivary syringe with a piston pump.
   O. Hypopharynx a brace or guide for mandibular and maxillary stylets.
   P. Hypopharynx a membranous surface.
   Q. Hypopharynx a bulbous reservoir of chitinized structures and terminating in an aperturate lobe.
   R. Hypopharynx a sclerotized, molar-like structure bearing teeth.

26. **Epipharynx type.**
   A. Epipharynx absent.
   B. Epipharynx lingulate or spatulate; fleshy.
   C. Epipharynx setate or bearing bristles.
   D. Epipharynx stylate; adjoined to the labrum.
   E. Epipharynx membranous.
   F. Epipharynx haustellate; fused to labrum.
   G. Epipharynx denticulate or spinose.
   H. Epipharynx forming the ventral part of a food pump, with a sensory organ and prelabral gutter.
   I. Epipharynx lobate, bordered by setae.
   J. Epipharynx molariform (e.g. a "pestle").
   K. Epipharynx penicillate or fimbrate.
   L. Epipharynx the ventral part of a food pump, with a sensory organ and a postlabral beak brace.
   M. Epipharynx bearing a pair of sclerotized rods or sclerites.
   N. Epipharynx sulcate, bordered by setae.

VII. MANDIBULAR REGION [GROUP VII]

27. **Mandibular articulation.**
   A. Mandibles absent, vestigial, or diminutive.
   B. Articulation monocondylic.
   C. Articulation dicondylic.
   D. Articulation acondylic, a lever system for protraction and retraction.
   E. Articulation acondylic, mandibles attached directly to retractor musculature; no lever system.
   F. Mandibles dicondylic, condyles (preartis/postartis) rotated normal to mandibular axis.

28. **Mandibular type** (shape of body).
   A. Mandibles absent, vestigial, or diminutive.
   B. Mandibles tetragonal and three-dimensional in mesad or laterad profile.
   C. Mandibles securiform; distally-expanded.
   D. Mandibles quadrangular and three-dimensional in mesad or laterad profile.
   E. Mandibles fused to maxillae.
   F. Mandibles moderately falcate.
   G. Mandibles extremely falcate; cultriform.
   H. Mandibles ensiform; long laminate blades.
   I. Mandibles stylate-elongate, housed in a haustellum and relatively long.
   J. Mandibles tubulate and falcate, without appressed, articulating elements.
   K. Mandibles aciculate; stilletto-shaped.
   L. Mandibles ratchet-shaped, with prominent curved teeth and a plumose, retrally-directed process.
   M. Mandibles lamellate; consisting of a flexible, lamellate flap.
   N. Mandibles excavate; U-shaped in cross section.
   O. Mandibles short and hooklike (e.g. nontubulate larval mouth-hooks); psittaciform.
   P. Mandibles grooved and falcate, with two appressed and articulating elements.
   Q. Mandibles prolonged to elongate.
   R. Mandibles palmate.
   S. Mandibles cupulate.
29. **Mandibular dentition.**
   A. Mandibles absent, vestigial or diminutive.
   B. Mandibles edentate.
   C. Dentition dominated by a molariform region (e.g. a mola).
   D. Dentition dominated by an incisiform region.
   E. Dentition dominated by both molariform and incisiform regions.
   F. Dentition dominated by pronounced pectinate processes (e.g. coarse setae and diatom rakes).
   G. Dentition chelate; one tooth fixed and the other movable.
   H. Dentition prosthecate; dominated by a an articulating, fimbrate sclerite.
   I. Dentition serrated.
   J. Dentition dominated by (a) large, procumbent canine(s); molar and incisor regions present.
   K. Dentition dominated by a single, pronounced canine (retinaculum or lacinia mobilis) basally.
   L. Dentition with acuminate incisor(s) and a prominent mesial brush associated with a molar region.
   M. Dentition psittaciform; unmolarized and with a single, talon-like, terminal incisor.
   N. Dentition lophodont; with several subparallel, molar ridges.
   O. Dentition hamate; with barbs, barbules or backwardly-directed ridges.
   P. Dentition with a single, large, procumbent canine; molar region absent.
30. **Motion of mandibular musculation.**
   A. Musculation absent or vestigial.
   B. Musculation adduction/abduction (chewing); power stroke normal to sagittal plane.
   C. Musculation adduction/abduction (piercing-sucking); power stroke normal to sagittal plane.
   D. Musculation protraction/retraction (piercing-sucking); power stroke parallel to sagittal plane.
   E. Musculation adduction/abduction (chewing, piercing-sucking); power stroke vertical sagittally.
31. **Mandibular participation in a multielement mouthpart structure.**
   A. Participation lacking.
   B. Mandibles are part of a mandibulo-canaliculate complex (larvae of Neuroptera, Coleoptera & Diptera).
   C. Mandibles are styli in a fasiculate or labellate haustellum.
   D. Mandibles are part of a rostrum; apically located.
   E. Mandibles are part of a mouthcone, buccal cone, or labral cone.
   F. Mandibles are styli in a nonhaustellate beak.
   G. Mandibles are styli in a segmented haustellum.

VIII. MAXILLARY REGION [GROUP VIII]

32. **General condition of the stipes** (sclerotized portion).
    - A. Stipes absent or unrecognizable.
    - B. Stipes equant; squarose to trapezoidal (length/width between 0.5 and 2.0).
    - C. Stipes elongated: rectangular to trapezoidal (length/width between 2.0 and 4.0).
    - D. Stipes considerably elongated and rodlike (length/width greater than 4.0).
    - E. Stipes fused to adjacent structures (i.e. interstipital fusion or stipes/mandible fusion).
    - F. Stipes forming the maxillary plate.
    - G. Stipes transversely elongated.
33. **Maxillary main body segmentation** (including maxillary sclerite but excluding palpifer).
    - A. Main body absent, unrecognizable, or covered.
    - B. Main body comprising one sclerite, or cardo and stipes undifferentiated.
    - C. Main body comprising two sclerites: undifferentiated cardo, and a stipes.
    - D. Main body comprising three sclerites: paracardo, eucardo & cardo; or cardo, stipes & prestipes.
    - E. Main body comprising four sclerites: paracardo, eucardo, stipes and parastipes.
34. **Maxillary appendages.**
    - A. Appendages absent.
    - B. Maxilla bearing a galea only.
    - C. Maxilla bearing a lacinia only.
    - D. Maxilla bearing an undifferentiated, conjoined galea and lacinia.
    - E. Maxilla bearing a galea and lacinia only, each differentiated.
    - F. Maxilla bearing a palpus only.
    - G. Maxilla bearing a galea, a lacinia, and a palpus.
    - H. Maxilla bearing a fused galea and lacinia (=mala), and a palpus.
    - I. Maxilla bearing a "mala,"a a palpus, and a stylet (e.g. Thysanoptera).
    - J. Maxilla bearing a galea and a palpus only.
    - K. Maxilla bearing a lacinia and a palpus only.
35. **Maxillary palpus segmentation** (excluding palpifer and including palpal cone).
    - A. Maxillary palpus absent or vestigial.
    - B. Segmentation one in number (unsegmented).
    - C. Segmentation two in number.
    - D. Segmentation three in number.
    - E. Segmentation four in number.
    - F. Segmentation five in number.
    - G. Segmentation six or more in number.
36. **Maxillary palpus type.**
    - A. Maxillary palpus absent or vestigial.
    - B. Maxillary palpus mucronate.
    - C. Maxillary palpus filiform: linear to moderately clavate distally.
    - D. Maxillary palpus filiform: strongly clavate distally.
    - E. Maxillary palpus serrate.
    - F. Maxillary palpus pectinate of pinnate or radiate setae, spines, or fleshy projections.
    - G. Maxillary palpus bearing a region of dense hair or bristles modified into a brush.
    - H. Maxillary palpus with an enlarged middle segment (e.g. *Paussus*).
    - I. Maxillary palpus diminutive and resembling a seta, or aciculate.
    - J. Maxillary palpus stubby or papillate.
    - K. Maxillary palpus a tapering, setate lobe appressed to the mala.

37. **Maxillary palpus aspect ratio** (excluding palpifer and including palpal cone).
    - A. Maxillary palpus absent or vestigial.
    - B. Maxillary palpus long: length between eight and sixteen times the average palp width.
    - C. Maxillary palpus intermediate: length between four and eight times average palp width.
    - D. Maxillary palpus short: length less than four times average palp width.
    - E. Maxillary palpus very long: length greater than sixteen times average palp width.
38. **Galeal modifications.**
    - A. Galea absent, vestigial, or covered.
    - B. Galea generalized and unmodified: a fleshy lobe.
    - C. Galeae conjoined into a lever for protraction of lacinial stylets.
    - D. Galea stylate, not in a beak complex (e.g. Protura, Anoplura).
    - E. Galeae conjoined and siphonate (e.g. Lepidoptera, some Coleoptera).
    - F. Galea lingulate or spatulate (a single lobe).
    - G. Galea palpiform; often subsegmented.
    - H. Galea penicillate.
    - I. Galea pectinate (a rake or comb).
    - J. Galea lobate, with terminal sensillae and setae (larval Lepidoptera).
    - K. Galeae tubulate when apressed; bladelike and amplexiform (e.g. apoid Hymenoptera).
    - L. Galea mandibulate; a dentate lobe.
    - M. Galea vaginate.
    - N. Galea fused to the lacinia, bearing pectinate bristles mesially and a raker distally.
    - O. Galea fused to the lacinia, lobate and generalized.
    - P. Galeae long and cylindrical, with terminal or longitudinal setae or a spine.
    - Q. Galea fused to the lacinia, penicillate or fimbrate.
    - R. Galea part of mouthcone or oral cone wall (Thysanoptera).
    - S. Galea a lobate rasp.
39. **Lacinial modifications.**
    - A. Lacinia absent, vestigial, or covered.
    - B. Lacinia generalized and unmodified; mostly a fleshy lobe.
    - C. Lacinia lingulate or spatulate; a single lobe.
    - D. Lacinia stylate-acuminate and relatively short (e.g. Thysanoptera).
    - E. Lacinia stylate-acuminate and long, of one blade; rarely cruminate (e.g. Heteroptera).
    - F. Lacinia stylate-acuminate and short, consisting of two blades (e.g. Protura).
    - G. Lacinia fused to galea; a generalized, nonsetate lobe.
    - H. Lacinia fused to galea; a penicillate mala.
    - I. Lacinia elongate and fleshy; palpiform.
    - J. Lacinia penicillate or fimbrate (a brush).
    - K. Lacinia a pectinate comb, with mesially-directed setae or spines.
    - L. Lacinia mandible-like or a dentate to denticulate lobe (e.g. capitulum of Collembola).
    - M. Lacinia a falcate-shaped, pectinate lobe, with mesially-directed, acuminate spines.
    - N. Lacinia a single, grooved, falcate blade.
    - O. Lacinia straight, stylate, and grooved (channelled).
    - P. Lacinia a single pronounced seta or spine.
    - Q. Lacinia fused with the galea and pectinate, bearing spines or setae.
    - R. Lacinia mucronate.
    - S. Lacinia a long, sclerotized, protractile rod; the "maxillary pick" of Psocoptera and Mallophaga.

40. **Maxillary participation in a multielement mouthpart structure.**
    A. Participation lacking.
    B. Maxillae part of a channelled mandible/maxilla complex (e.g. larval Neuroptera, Coleoptera).
    C. Maxillae part of a labellum or labellum-like complex.
    D. Maxillae part of a rostrum.
    E. Maxillae part of a mouthcone, buccal cone, or labral cone.
    F. Maxillae as a stylet or stylets in a nonhaustellate beak.
    G. Maxillae as stylets in a segmented haustellum.
    H. Maxillae as stylets in a nonsegmented (fasiculate) haustellum.
    I. Maxillae part of a siphonate proboscis.
    J. Maxillae part of a glossate proboscis.
    K. Maxillae adjoined to labium as a single unit (maxillolabial complex).

IX. LABIAL REGION [GROUP IX]

41. **General shape and condition of labial main body** (submentum, mentum & prementum, minus gula & ligula).
    A. Labium absent or vestigial.
    B. Shape transversely elongate (sagittal length/width less than 0.5).
    C. Shape equant; squarose to trapezoidal (sagittal length/width between 0.5 and 2.0).
    D. Shape elongated; trapezoidal to rectangular (sagittal length/width between 2.0 and 4.0).
    E. Shape considerably elongated; rod-like (sagittal length/width greater than 4.0).
42. **Labial main body segmentation** (excluding palpiger).
    A. Labium absent or vestigial.
    B. Labium of one segment only: basimentum and prementum undifferentiated.
    C. Labium of two segments: basimentum (submentum + mentum) and prementum, or submentum and mentum.
    D. Labium of three segments: submentum, mentum and prementum.
    E. Labium the first segment on a multisegmented beak.
43. **Labial appendages.**
    A. Appendages absent or vestigial.
    B. Glossae, ligula, or other unappendiculate sclerite only.
    C. Paraglossae and labial palps only.
    D. Glossae and labial palps/labellum only.
    E. Labial palps/labellum only.
    F. A medial terminal projection (ligula, spinneret) and labial palps.
    G. Glossae, paraglossae, and labial palps.
44. **Labial palpus segmentation** (excluding palpiger; including palpal cone).
    A. Labial palps absent or vestigial.
    B. Segmentation one in number (unsegmented).
    C. Segmentation two in number.
    D. Segmentation three in number.
    E. Segmentation four or more in number.

45. **Labial palpus type.**
    A. Labial palpus absent or vestigial.
    B. Labial palpus mucronate.
    C. Labial palpus clavate.
    D. Labial palpus filiform.
    E. Labial palpus pectinate, modified into a coarse comb of setae, spines or fleshy projections.
    F. Labial palpus penicillate.
    G. Labial palpus chelate, with a single, distal raptorial hook.
    H. Labial palpi forming a tubular passage when conjoined (e.g. Apoidea).
    I. Labial palpi tubular, with apical denticles or acuminate (astylate).
    J. Labial palpus papillate to stubby.
    K. Labial palpi labellate, or forming a similar structure; without stylate denticles.
    L. Labial palpus aciculate or setate.
    M. Labial palpus chelate, with a movable and an immovable hook distally.
    N. Labial palpus serrate.
    O. Labial palpus squamate.
    P. Labial palpus with an enlarged or ligulate middle segment (e.g. *Tricondylia*).
    Q. Labial palpi are appressed, forming a sheath for housing stylets.
    R. Labial palpi labellate, with stylate denticles.
46. **Glossae modifications.**
    A. Glossae [or ligula] absent or vestigial.
    B. Glossae [or ligula] generalized and unmodified; a broadly-attached, lingulate lobe (fused).
    C. Glossae [or ligula] lingulate or spatulate; each a single lobe (separate).
    D. Glossae [or ligula] stylate, or glossa and paraglossa fused to form a stylet.
    E. Glossae [or ligula] scrobinate (rasp).
    F. Glossae [or ligula] mucronate.
    G. Glossae [or ligula] an intermediate-length to long, flabellate tongue (e.g. apoid Hymenoptera).
    H. Glossae [or ligula] setate.
    I. Glossae [or ligula] two or more generalized lobes.
    J. Glossae [or ligula] fused to paraglossae as a generalized ligula.
    K. Glossae [or ligula] bearing silk glands at their ductal openings (silk press).
    L. Glossae [or ligula] penicillate (brush).
    M. Glossae [or ligula] papillate.
    N. Glossae [or ligula] aciculate or bearing spines.
    O. Glossae [or ligula] broadly attached and a platelike lobe.
    P. Glossae [or ligula] participating in formation of an oral cone.
47. **Paraglossae modifications.**
    A. Paraglossae absent or vestigial.
    B. Paraglossae generalized and unamodified; mostly a fleshy lobe (fused).
    C. Paraglossae lingulate or spatulate; each a single lobe or lobes (separate).
    D. Paraglossae pectinate.
    E. Paraglossae as basal glossal coverlets.
    F. Paraglossae mucronate.
    G. Paraglossae forming a long, flabellate tongue.
    H. Paraglossae fused with glossae as a generalized lingulate ligula.
    I. Paraglossae a broadly attached, platelike lobe.
    J. Paraglossae penicillate.
    K. Paraglossae participating in formation of an oral tube.

48. **Labial palpus aspect ratio** (excluding palpiger; including palpal cone).
    - A. Labial palpus absent or forming a labial sheath.
    - B. Length long: total palpus length between 8.0 and 16.0 times average palpus width.
    - C. Length intermediate: total palpus length between 4.0 and 8.0 times average palpus width.
    - D. Length short: total palpus length less than 4.0 times average palpus width; nonlabellate.
    - E. Length short: total palpus length less than 4.0 times average palpus width; labellate.
    - F. Length very long: total palpus length greater than 16 times average palpus width.

49. **Labial participation in a multielement mouthpart structure.**
    - A. Labial participation lacking.
    - B. Labium part of the mouthcone, buccal cone, or labral cone (e.g. Thysanoptera, some Coleoptera).
    - C. Labium a segmented haustellum.
    - D. Labium an unsegmented (fasiculate) haustellum.
    - E. Labium fleshy, distally expanded, or supporting such a structure; without stylate denticles.
    - F. Labium a raptorial protrusible mask (larval Odonata and *Stenus*).
    - G. Labium part of a gnathal pouch (e.g. Protura, Anoplura).
    - H. Labium part of a rostrum.
    - I. Labium a guide, channel, or support for stylet movement.
    - J. Labium a support for a maxillary siphon.
    - K. Labium a tubular support for a glossate proboscis.
    - L. Labium a long, tubular stylet with apical teeth.
    - M. Labium a silk gland complex (with hypopharynx).
    - N. Labium adjoined to maxilla as a single unit (maxillolabial complex).
    - O. Labium fleshy, distally expanded, with an armature of numerous stylate denticles.

DIETARY DATA

X. FEEDING CLASS

50. **Functional feeding group.**
    - A. Piercing-sucking: subdermal tissue (e.g. vascular tissue). Deep stylet penetration.
    - B. Piercing-sucking: dermal tissue (e.g. epidermis). Surface stylet laceration and penetration.
    - C. Rasping-and-sucking.
    - D. Grasping-and-sucking, biting-and-piercing (through a mandibular or mandibular/maxillary canal).
    - E. Chewing or cutting.
    - F. Crushing.
    - G. Rasping-and-chewing; scraping-and-chewing.
    - H. Chewing-and-lapping.
    - I. Lapping and squeezing.
    - J. Sponging.
    - K. Siphoning (nonpiercing).
    - L. Filter-feeding (comb-sieving with suction, including silk net traps).
    - M. Filter-feeding (brush-sweeping, scraping, or raking without suction).
    - N. Indeterminate.
    - O. Punch-and-sucking.
    - P. Grasping/piercing-and-sucking (mouth-hooks, without a mandibular canal).
    - Q. Feeding absent.
    - R. Boring.
    - S. Passive inflow or absorption.
    - T. Chewing and sucking.
    - U. Piercing-and-cutting.

XI. DIET CHARACTERIZATION

51. **Diet type** (trophically-based).

Herbivory (live plant tissue only).
- A. Herbivory undifferentiated.
- B. Granivory.
- C. Seminivory.
- D. Florivory.
- E. Folivory.
- F. Frugivory.
- G. Nectarivory (and other surface exudates, including sweat and honeydew).
- H. Pollenivory.
- I. Phytosuccivory (sap).
- J. Radicivory (including stems).
- K. Lignivory.
- !. Nectarivory and pollenivory.

Fungivory (live fungal tissue only).
- L. Fungivory undifferentiated.
- M. Sporivory.
- N. Mycelivory.
- O. Sporangivory.

Carnivory (live animal tissue only)
- P. Carnivory undifferentiated.
- Q. Insectivory (including arachnids and myriapods).
- R. Zoosuccivory (especially sanguinivory).
- S. Endoparasitic (body tissues).
- T. Ectoparasitic (skin, feathers, hair, etc.).
- =. Soft invertebrates (molluscivory; principally snails and worms).

Necrovory (dead tissue).
- U. Necrovory undifferentiated.
- V. Necroherbivory (e.g. leaf detritus, rotting fruit).
- W. Necrocarnivory (e.g. carrion).
- X. Stercovory.
- Y. Necrofungivory.
- Z. Necrolignivory (e.g. rotting wood, starch).

Detrivory.
- *. Detrivory (bacteria, protists, yeasts, algae, rotifers, cladocerans, suspended food fragments.

Omnivory.
- &. Generalized omnivory (eclectic diets with components from two or more organismic kingdoms).

Unique diets.
- #. Ceravory (wax; e.g. *Galleria*, a moth).
- $. Pilivory (hair, wool, keratin; e.g. *Anthrenus*, a dermestid beetle).
- +. Freshwater sponges (e.g. some aquatic larval Plannipennians).

Nontrophy.
- %. Food is not ingested (e.g. adult male Embioptera, adult Ephemoptera and male Coccoidea).
- /. Limnivory (mud/water suspension).
- @. Regurgitated liquid (trophallaxis in social insects; honey, royal jelly).

52. **Diet breadth.**
    - A. Diet stenophagous (food confined to same genus).
    - B. Diet mesophagous (food confined to same family).
    - C. Diet euryphagous (food confined to more than one family).
    - D. Diet breadth indeterminate.
    - E. Diet absent.
53. **Form of the food.**
    - A. Food absent.
    - B. Food as a fluid.
    - C. Food as small, suspended particles or organisms.
    - D. Food as a solid (fleshy or most of the item is eaten as pieces).
    - E. Food as a fluid/solid mixture, or both individually.
    - F. Form of the food indeterminate.

LABELS

XII. HABITAT AND LIFE PARAMETERS

54. **General habitat.**
    - A. Habitat indeterminate.
    - B. Habitat aquatic (in or on top of the water).
    - C. Habitat semiaquatic, or amphibious (near the water, or periodically subaqueous).
    - D. Habitat terrestrial: ground-dwelling.
    - E. Habitat terrestrial: associated with plants or fungi.
    - F. Habitat terrestrial: associated with animals.
    - G. Habitat fossorial (subterranean).
55. **Growth stage.**
    - A. Growth stage indeterminate.
    - B. Growth stage a naiad (aquatic and hemimetabolous).
    - C. Growth stage a nymph (terrestrial and hemimetabolous).
    - D. Growth stage a larva (holometabolous).
    - F. Growth stage an adult.
56. **Sex and caste.**
    - A. Sex unknown, undocumented, or combination of both sexes used in the determination.
    - B. Sex a female, including queen, worker and alate castes.
    - C. Sex a male, including king, worker and drone castes.
    - D. Sex undifferentiated, including soldier and nasute castes.

APPENDIX B

REFERENCE LIST OF INSECT TAXA DESCRIBED BY MOUTHPART MORPHOLOGY AND DIETARY DATA*

taxon	mouthpart morphology data	dietary data	no.
PROTURA			
Acerentomidae			
Acerentomon doderoi Silvestri	Snodgrass 1950; [Francois 1959, 1969]; Tuxen 1959, [1962]; [Schaller & Wolter 1963]; Richards & Davies 1977	Sturm 1959; Richards & Davies 1977; Moore 1988	1.
Acerentulus tiarneus	Metcalf 1929; [Tuxen 1959]	Sturm 1959; Richards & Davies 1977	2.
Proentomidae			
Sinentomidae			
Eosentomidae			
Eosentomon transitorium Berlese	[Crampton 1923b]; [Snodgrass 1950]; Francois 1969; Smith 1985	Sturm 1959; Richards & Davies 1977; Moore 1988	3.
COLLEMBOLA			
So. Arthropleona			
Sf. Hypogastruoidea			
Onychiuridae			
Onychiurus armatus Tullberg	Denis 1928; Tuxen 1959	Poole 1959	4.
Hypogastruridae			
Sf. Entomobryoidea			
Entomobryidae			
Orchesella cincta Linneaus	Folsom 1899; [Matsuda 1965]; [Richards & Davies 1977]	Fitch 1863; Poole 1959	5.
Isotomidae			
Folsomia candida	Goto 1972	Poole 1959; Goto 1972	6.
Oncopoduridae			
Tomoceridae			
Tomocerus longicornis (Müller)	[Hoffman 1905, 1908, 1911]; [Crampton 1923b]; [Denis 1928]; [Snodgrass 1928]; [Schaller & Wolter 1963]; [Wolter 1963]; Manton 1964, 1977; [Matsuda 1965]	Poole 1959; Wolter 1963	7.

---

*Notes: Taxa with asterisks are immature forms. Brackets indicate secondary data sources from congeneric species of the genus indicated. Classification is from Parker (1982; Appendix D).

taxon	mouthpart-morphology data	dietary data	no.
So. **Neoarthropleona**			
Brachystomellidae			
Brachystomella parvula (Schaeffer)	Adams & Salmon 1972	Adams & Salmon 1972	8.
Anuridae			
Anurida maritima (Guerin)	Folsom 1900; Hosford 1913; Crampton 1923b; Denis 1928; Snodgrass 1950, 1960; Schaller & Wolter 1963; Wolter 1963; Cassagnau & Juberthie 1967	McNamara 1924; Wolter 1963	9.
Setanuridae			
Neanuridae			
Neanura muscorum (Templeton)	Schaller & Wolter 1963; Wolter 1963; Richards & Davies 1977	Poole 1959, Wolter 1963	10.
Uchidanuridae			
So. **Metaxypleona**			
Poduridae			
Actaletidae			
So. **Sympleona**			
Neelidae			
Sminthuridae			
Deuterosminthurus quinquefasciatus (Krausbauer)	Jeannenot 1956	Jeannenot 1956	11.
DIPLURA			
So. **Rhabdura**			
Sf. **Projapygoidea**			
Anajapygidae			
Projapygidae			
Sf. **Campodeoidea**			
Procampodeidae			
Campodeidae			
Campodea chardardi Condé	[Evans 1921]; [Crampton 1923b]; [Snodgrass 1947]; [Bitsch 1952]; [Tuxen 1959]; [Manton 1964, 1977]; Francois 1970	Arnett 1985	12.
So. **Dicellurata**			
Sf. **Japygoidea**			
Japygidae			
Heterojapyx gallardi	Snodgrass 1928, 1935, 1950, 1960; Richards & Davies 1977	Kosaroff 1935	13.
Japyx major (Grassi)	[Crampton 1923b]; Silvestri 1933; [Tuxen 1971]; [Bitsch & Denis 1973]	Kosaroff 1935	14.
Parajapygidae			

taxon	mouthpart-morphology data	dietary data	no.
ARCHAEOGNATHA			
Machilidae			
Machilus sp.	Crampton 1921b, 1921c, 1921d, 1923b; [Evans 1921]; Snodgrass 1928, 1932; Walker 1931a, 1932; Ferris 1942; Chaudonneret 1956; Bitsch 1960, 1963; DuPorte 1962; Manton 1964, 1977; Tuxen 1971	Arnett 1985	15.
Petrobius brevistylus Carpenter	[Evans 1921]; Bitsch 1956; Manton 1977; Matsuda 1965; Richards & Davies 1977	Manton 1977	16.
Meinertellidae			
Nesomachilus maoricus Tillyard	Snodgrass 1928, 1935, 1950; Boudreaux 1979	Arnett 1985	17.
THYSANURA			
Lepidotrichidae			
Tricholepidon gertschi Wygodzinsky	Wygodzinsky 1961	Wygodzinsky 1961	18.
Lepismatidae			
Acrotelsa collaris (Fabricius)	Modder 1969	Modder 1969	19.
Ctenolepisma longicaudata Eschscholtz	[Walker 1932]; [Snodgrass 1950]; Manton 1964, 1977	Arnett 1985	20.
Lepisma sp.	[Borner 1909]; Crampton 1917a, 1917b; [Evans 1921]; Snodgrass 1928; Ferris 1942; DuPorte 1946; Matsuda 1965; Larinck 1970; Manton 1977	Howard 1905; Clausen 1940	21.
Thermobia domestica (Packard)	[Snodgrass 1928]; Walker 1931a; O'Hara & Adams 1942; Chaudonneret 1948, 1950; Noars 1961; Tuxen 1962; Boudreaux 1979	Howard 1905; Atkins 1978	22.
Maindroniidae			
Nicoletiidae			
Protrinemura mediterranea Mendes	Mendes 1988	Mendes 1988	23.
EPHEMEROPTERA			
So. Schistonota			
Sf. Baetoidea			
Siphlonuridae			
*Ameletus inopinatus** Eaton	Murphy 1922; Crampton 1928; Day 1956; Landa 1969	diet undocumented	24.
*Siphlonurus lacustris** (Eaton)	Spieth 1933; [Cook 1944]; Landa 1969; [Schonmann 1981]	Morgan 1913; Needham, Traver & Hsu 1935	25.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
Ametropodidae			
*Ametropus fragilis** Albarda	Landa 1969	Ross 1965	26.
Baetidae			
*Baetis rhodani** Pictet	Sternfeld 1907; Borner 1909; Day 1956; Brown 1961; Noars 1961; Landa 1969	Murphy 1922; Brown 1961; Milne & Milne 1980; Chessman 1986	27.
*Chloeon dipterum** Linneaus	Sternfeld 1907; Borner 1909; [Berlese 1909]; Evans 1921; Spieth 1933; Vassal 1947; Day 1956; Brown 1969; Landa 1969	Murphy 1922; Brown 1961; Chessman 1986	28.
Metretopodidae			
Oligoneuridae			
*Oligoneuriella rhenana** (Imhoff)	Landa 1969	diet undocumented	29.
*Isonychia ignota** (Walker)	Landa 1969; [Braimah 1987a, 1987b]	Needham, Traver & Hsu 1935	30.
Heptageniidae			
*Arthroplea congener** Bengtsson	Needham, Traver & Hsu 1935; Froehlich 1964; Landa 1969	Froehlich 1964	31.
*Ecdyonurus helveticus** (Eaton)	Spieth 1933; Strenger 1954; Landa 1969	Ross 1965	32.
*Ecdyurus** sp.	Murphy 1922	Ross 1965	33.
*Heptagenia flava** Rostock	[Packard 1898]; [Crampton 1921b];	Morgan 1913; Murphy 1922	34.
*Lepeorus goyi** Peters	Schonmann 1981	Needham, Traver & Hsu 1935	35.
*Stenonema vicarium** Walker	Needham, Traver & Hsu 1935	Needham, Traver & Hsu 1935	36.
Stenonema vicarium Walker	Needham, Traver & Hsu 1935	Needham, Traver & Hsu 1935	37.
Sf. Leptophlebiioidea			
Leptophlebiidae			
*Habroleptoides modesta** (Hagen)	Landa 1969	diet undocumented	38.
*Leptophlebia** sp.	Spieth 1933; Snodgrass 1950	Milne & Milne 1980	39.
*Paraleptophlebia submarginata** (Stephens)	Needham, Traver & Hsu 1935; Landa 1969	Milne & Milne 1980; [Mattingly 1987b]	40.
*Rithrogenia** sp.	Strenger 1954; Day 1956; Landa 1969	Murphy 1922; Milne & Milne 1980	41.
Sf. Ephemeroidea			
Behningiidae			
*Behningia ulmeri** Lestage	Landa 1969	diet undocumented	42.

taxon	mouthpart-morphology data	dietary data	no.
Potamanthidae			
*Potamanthus luteus** (Linneaus)	[Morgan 1913]; Landa 1969; Borror, DeLong & Triplehorn 1976	Comstock 1977	43.
Euthyplociidae			
Polymitarcyidae			
*Ephoron virgo** (Olivier)	Landa 1969	Comstock 1977	44.
Ephemeridae			
*Ephemera vulgata** Linneaus	[Morgan 1913]; Murphy 1922; [Spieth 1933]; [Day 1956]; Landa 1969	Murphy 1922; Milne & Milne 1980	45.
Hexagenia recurvata Morgan	[Sternfeld 1907]; Murphy 1922; Needham, Traver & Hsu 1935	Morgan 1913; Milne & Milne 1980	46.
*Hexagenia** sp.	Murphy 1922; Spieth 1933; Snodgrass 1950	Morgan 1913; Milne & Milne 1980	47.
Palengeniidae			
*Palingenia longicauda** (Olivier)	Landa 1969	Comstock 1977	48.
So. Pannota			
Sf. Ephemerelloidea			
Ephemerellidae			
*Ephemerella ignita** (Poda)	Landa 1969	Milne & Milne 1980	49.
Tricorythidae			
Sf. Caenoidea			
Neoephemeridae			
Caenidae			
*Caenis macrura** Stephens	Landa 1969	Morgan 1913	50.
Baetiscidae			
Sf. Prosopistomatoidea			
Prosopistomatidae			
*Prosopistoma foliaceum** (Fourcroy)	Needham, Traver & Hsu 1935; Landa 1969	Morgan 1913; Needham, Traver & Hsu 1935	51.
ODONATA			
So. Zygoptera			
Sf. Lestinoidea			
Perilestidae			
Chlorolestidae			
Lestidae			
Lestes barbarus (Fabricius)	Butler 1904; [Lew 1933]; Strenger 1952; [Asahina 1954]; [Hakim 1964]	Milne & Milne 1980	52.
Sf. Hemiphleboidea			
Hemiphlebiidae			
Sf. Coenagrionoidea			
Platystictidae			
Megapodagrionidae			
Protoneuridae			
Platycnemidae			

taxon	mouthpart-morphology data	dietary data	no.
Lestoideidae			
Coenagrionidae			
*Agrion hastulatum** Charpentier	Munscheid 1933; [Corbet 1953]; [Callière 1972]	Comstock 1940	53.
Pseudagrion decorum (Rambur)	Hakim 1964; Denis & Bitsch 1973	Clausen 1940; Chutter 1961	54.
Pseudostigmatidae			
Sf. Calopterygoidea			
Amphipterygidae			
Chlorocyphidae			
Heliocharitidae			
Polythoridae			
Epallagridae			
Calopterygidae			
Mnais strigata Selys	Asahina 1954	Comstock 1977	55.
So. Anisozygoptera			
Epiophlebiidae			
*Epiophlebia superstes** Selys	Lew 1933; Asahina 1954	Asahina 1950	56.
Epiophlebia superstes Selys	Lew 1933; Asahina 1954	Asahina 1950	57.
So. Anisoptera			
Sf. Aeshnoidea			
Gomphidae			
Davidius nanus Selys	Asahina 1954	[Milne & Milne 1980]	58.
Gomphus agricola Linneaus	Lew 1933; [Denis & Bitsch 1973]	[Milne & Milne 1980]	59.
Ictinogomphus rapax (Rambur)	Hakim 1964	[Milne & Milne 1980]	60.
Ictinus angulosus Selys	Mathur & Mathur 1961b	[Milne & Milne 1980]	61.
Onychogomphus ardens Needham	Chao 1953	[Milne & Milne 1980]	62.
Petaluridae			
Aeshnidae			
*Aeshna cyanea** Müller	[Crampton 1923b]; [Lucas 1924]; Short 1955; [Popham & Bevons 1979]; Tanaka & Hisada 1980	Claassen 1930	63.
Aeshna juncea Linneaus	[Crampton 1923b]; [Lucas 1923/1924]; [Snodgrass 1928]; Munscheid 1933; [Corbet 1953]; Popham & Bevons 1979; Tanaka & Hisada 1980	Claassen 1930	64.
*Anax junius** (Drury)	Butler 1904; Whedon 1927; Lew 1933; Snodgrass 1947, 1960; [Asahina 1954]; Watson 1955	Kasimov 1956; Swann & Papp 1972; Milne & Milne 1980	65.
Anax junius (Drury)	Lew 1933; Snodgrass 1954	Poulton 1906; Milne & Milne 1980	66.

taxon	mouthpart-morphology data	dietary data	no.
Sf. Cordulegasteroidea			
Cordulegasteridae			
Cordulegaster boltoni (Donovan)	Butler 1904; [Lew 1933]; Corbet 1953; Smith & Pritchard 1956; Richards & Davies 1977	[Poulton 1906]; Milne & Milne 1980	67.
Sf. Libelluloidea			
Synthemidae			
Corduliidae			
Libellulidae			
Brachythemis contaminata Fabricius	Mathur 1956; Hakim 1964	Pritchard 1964	68.
Crocothemis servilia (Drury)	Asahina 1954; Hakim 1964	[Poulton 1906]; Pritchard 1964	69.
*Libulellula quadrimaculata** Linneaus	Marshall 1914; [Lucas 1923/1924]; Pritchard 1964, 1976; Popham & Bevons 1979	Pritchard 1964	70.
Libellula quadrimaculata Linneaus	[Smith 1898]; Marshall 1914; [Walker 1931a]; [Lew 1933]	Poulton 1906; Pritchard 1964	71.
Orthetrum taeniolatum Schneider	[Butler 1904]; [Corbet 1953]; [Asahina 1954]; Mathur & Mathur 1961a	Poulton 1906	72.
Pantala flavescens Fabricius	Mathur 1962	Warren 1915	73.
BLATTODEA			
Cryptocercidae			
Cryptocercus punctulatus Scudder	Cleveland 1934	Cleveland 1934	74.
Blattidae			
Blatta orientalis Linneaus	Smith 1898; Berlese 1909; Yuasa 1920; Crampton 1921c; Eidmann 1925; Snodgrass 1932, 1935, 1944, 1950; Strenger 1942; Schmitz 1945; Denis & Bitsch 1973; Richards & Davies 1977	Milne & Milne 1980	75.
Periplaneta americana (Linneaus)	Berlese 1909; [Mangan 1909]; [Bugnion 1920]; Golden 1925]; Crampton 1923b, 1925; Snodgrass 1928, 1944; Walker 1931a; Dorsey 1943; Popham 1961; Roberts 1975	Costa Lima 1968; Milne & Milne 1980	76.
Polyphagidae			
Blatellidae			
Blatella germanica Linneaus	Borner 1909; [Walker 1932]; [Ferris 1942]; Hoyt 1942; Snodgrass 1943, 1944	Costa Lima 1968; Milne & Milne 1980	77.

taxon	mouthpart-morphology data	dietary data	no.
Parcoblatta pensylvanica (DeGeer)	Walker 1933; Gangwere 1965	Gangwere 1965	78.
Blaberidae			
Blaberus cranifer Burmeister	Jeannel 1949; Moulins 1971	Arnett 1985	79.
MANTODEA			
Chaeteessidae			
Metallyticidae			
Mantoididae			
Eremiaphilidae			
Eremiaphila sp.	Crampton 1932	Fernald 1935	80.
Amorphoscelidae			
Hymenopodidae			
Empusidae			
Mantidae			
Mantis religiosa (Linneaus)	Suslov 1912; Hosford 1913; Yuasa 1920; Strenger 1942; [Hudson 1945]; DuPorte 1946	Clausen 1940; Milne & Milne 1980	81.
Stagnomantis carolina (Johannson)	Crampton 1923b; Walker 1931a, 1933; Levereault 1936	Fernald 1935; Milne & Milne 1980	82.
Tenodera sinensis Saussure	Snodgrass 1947; Gangwere 1965	Hadden 1927; Thieroff 1928; Fernald 1935	83.
ISOPTERA			
Mastotermitidae			
Mastotermes darwiniensis Froggatt	Crampton 1921, 1932; Hare 1937;	Emerson 1965	84.
Kalotermitidae			
Kalotermes flavicollis Fabricius	Holmgren 1909; [Crampton 1932]; [Hare 1937]; [Ahmad 1950]; Richard 1951	Swan & Papp 1972	85.
Hodotermitidae			
Architermopsis sp.	Richards & Davies 1977	Richards & Davies 1977	86.
Termopsis, sp., soldier	Crampton 1921; Snodgrass 1932, 1935, 1960; Walker 1932; Ahmad 1950	Richards & Davies 1977	87.
Zootermopsis angusticollis (Hagen)	[Hare 1937]; Cook 1944; Ahmad 1950	Swan & Papp 1972; Milne & 1980	88.
Rhinotermitidae			
Rhinotermes taurus Desneux	Holmgren 1909; Jeannel 1949; [Ahmad 1950]	Richards & Davies 1977; [Hill 1983]	89.
Serritermitidae			
Serritermes serrifer (Hagen & Bates), soldier	Emerson & Krishna 1975	Emerson & Krishna 1975	90.
Termitidae			
Macrotermes gilvus	[Hare 1937]; Cook 1944; [Ahmad 1950]; Deligne 1965	Richards & Davies 1977	91.

taxon	mouthpart-morphology data	dietary data	no.
Nasutitermes chaquimayensis Holmgren	Holmgren 1909; [Ahmad 1950]; [Brues, Melander & Carpenter 1954]	Lubin 1983	92.
Odontotermes obesus (Rambur), alate	[Holmgren 1909]; [Ahmad 1950]; Vishnoi 1956; Roonwal & Sangal 1960	Hill 1983	93.
Odontotermes obesus (Rambur), worker	[Holmgren 1909]; [Ahmad 1950]; Vishnoi 1956; Roonwal & Sangal 1960	Hill 1983	94.
Odontotermes obesus (Rambur), soldier	[Holmgren 1909]; [Ahmad 1950]; Vishnoi 1956; Roonwal & Sangal 1960	Hill 1983	95.
GRYLLOBLATTODEA			
Grylloblattidae			
Grylloblatta campodeiformis Walker	Crampton 1917, 1923b, 1926; Walker 1931a, 1931b, 1933; Ferris 1942; Beier 1955	Richards & Davies 1977	96.
ORTHOPTERA			
So. Ensifera			
Sf. Stenopelmatoidea			
Lezinidae			
Stenopelmatidae			
Stenopelmatus sp.	Comstock & Kochi 1902; Hosford 1913; Yuasa 1920; Crampton 1930a, [1932]; Beier 1955	Swan & Papp 1972; Milne & Milne 1980	97.
Cooloolidae			
Cooloola propator Rentz	Rentz 1980, 1987	Rentz 1980; Kevan 1982a	98.
Gryllacrididae			
Gryllacris leefmansi Karny	Karny 1924, [1925]	Richards & Davies 1977	99.
Mimnermidae			
Sf. Raphidophoroidea			
Macropathidae			
Macropathus filifer Walker	Richards 1955	Richards & Davies 1977	100.
Raphidophoridae			
Tachycines asynamorus Adelmann	Beier 1955; Wada 1965	Richards & Davies 1977	101.
Sf. Hagloidea			
Prophlangopsidae			
Cyphoderris sp.	Zeuner 1939	Arnett 1985; [Kevan 1982a]	102.
Sf. Tettigonoidea			
Bradyporidae			
Acridoxenidae			

taxon	mouthpart-morphology data	dietary data	no.
Phaneropteridae			
Amblycorypha albifrons	[Isely 1944]; [Kramer 1944]; Gangwere 1960, [1965]	Milne & Milne 1980	103.
Pseudophyllidae			
Meconematidae			
Phasmodidae			
Phylloporidae			
Mecopodidae			
Mecopoda elongata (Linneaus)	[Karsch 1886]; Karny 1924	Hill 1983	104.
Tettigoniidae			
Decticus albifrons Serville	Berlese 1909; Strenger 1942	[Arnett 1945]	105.
Saga serrata Charpentier	[Golden 1925]; Strenger 1952; Beier 1955	[Williams 1954]; Uvarov 1966	106.
Conocephalidae			
Orchelimum vulgare (Harris)	Yuasa 1920; Gangwere 1965	Milne & Milne 1980	107.
Sf. Schizodactyloidea			
Schizodactylidae			
Sf. Gryllotalpoidea			
Gryllotalpidae			
Gryllotalpa gryllotalpa (Linneaus)	Crampton 1923a, [1923b, 1932]; LaGreca 1939; Strenger 1942; [Rakshpal 1954]; Beier 1955	Swan & Papp 1972	108.
Sf. Grylloidea			
Gryllidae			
Acheta domestica Linneaus	[Symmons 1952]; Rietschel 1953	Swan & Papp 1972; Hill 1983	109.
Gryllus pennsylvanicus Burmeister	Yuasa 1920; [Crampton 1921c, 1923b, 1932]; [Golden 1925]; [Walker 1931a, 1933]; [Snodgrass 1932]; [Ferris 1942]; [Strenger 1942]; [Hudson 1945]; [DuPorte 1946]; Gangwere 1965; [Matsuda 1965]; Borror, DeLong & Triplehorn 1976	Milne & Milne 1980	110.
Liogryllus campestris Linneaus	Golden 1925; Strenger 1942	Costa Lima 1968	111.
Pentacentridae			
Trigonidiidae			
Phlangopsidae			
Luzara minor Hebard	Hebard 1928	Hebard 1928	112.
Eneopteridae			
Scleropteridae			
Pteroplistidae			
Cachoplistidae			
Mogoplistidae			
Myrmecophilidae			
Myrmecophila acervorum Panzer	Schimmer 1909	[Richards & Davies 1977]	113.
Oecanthidae			

taxon	mouthpart-morphology data	dietary data	no.
So. **Caelifera**			
Sf. **Eumastacoidea**			
Chlorotypidae			
Eruciidae			
Mastacideidae			
Euschmidtiidae			
Thericleidae			
Miraculidae			
Episactidae			
Eumastacidae			
Gomphomastacidae			
Biroellidae			
Morabidae			
Keyacris scurra (Rehn)	Blackith & Blackith 1966	Blackith & Blackith 1966	114.
Sf. **Prosopoidea**			
Prosopiidae			
Cephalocoema albrechti Zolessi	Zolessi 1968	Zolessi 1968; [Kevan 1982a]	115.
Sf. **Trigonopterygoidea**			
Boreacrididae			
Trigonopterygidae			
Sf. **Xyonotoidea**			
Syonotidae			
Tanaoceridae			
Tanaocerus koebelei Brunner	Rehn 1948; Grant & Rentz 1967	Rehn 1948	116.
Sf. **Pneumoroidea**			
Pneumoridae			
Bullacris unicolor Linneaus	Dirsch 1965	Dirsch 1965; [Kevan 1982a]	117.
Sf. **Acridoidea**			
Pamphagodidae			
Pamphagidae			
Tristiridae			
Lathiceridae			
Pyrgomorphidae			
Zonocerus variegatus (Linneaus)	Chapman & Thomas 1978; Hill 1983	Chapman & Thomas 1978	118.
Lentulidae			
Ommexechidae			
Ommexecha brunneri Bolivar	Gurney & Liebermann 1963	Gurney & Liebermann 1963; [Kevan 1982]	119.
Romaleidae			
Romalea microptera (Beauvois)	Evans 1984	Milne & Milne 1980	120.
Pauliniidae			
Marellia remipes Uvarov	Carbonell 1959	Swan & Papp 1972	121.
Acrididae			
Anacrydium aegyptium Linneaus	Strenger 1942	Strenger 1942; [Chapman & & Thomas 1978]	122.
Dissosteira carolina (Linneaus)	Crampton 1916; Snodgrass 1928	Swan & Papp 1972; Milne & Milne 1980	123.
Hippiscus sp.	Nininger 1915; Arnett 1985	diet undocumented	124.

taxon	mouthpart-morphology data	dietary data	no.
Locusta migratoria Linneaus	[Snodgdrass 1928]; Williams 1954; Manton 1964, 1977; Louveaux 1972, 1975	Williams 1954; Pruthi 1969; Hill 1983	125.
Melanoplus differentialis (Thomas)	[Comstock & Kochi 1902]; [Hosford 1913]; Nininger 1915; Yuasa 1920; [Walker 1931a, 1932]; [Gangwere 1965, 1966]	Swan & Papp 1972; Chapman & Thomas 1978; Milne & Milne 1980	126.
Schistocerca gregaria (Forskal)	[Nininger 1915]; [Golden 1925]; Williams 1954; Beier 1955; Thomas 1966	[Williams 1954]; Uvarov 1966; Swan & Papp 1972; Milne & Milne 1980	127.
Tryxalis nasuta Fischer	Strenger 1942	Strenger 1942	128.
Xenocheila zarundyni Uvarov	Chapman 1966	Chapman 1966	129.
Sf. Tetrigoidea			
Tetrigidae			
Tetrix arenosus Burmeister	Yuasa 1920; [Crampton 1923b]; [Gangwere 1965]	Richards & Davies 1977	130.
Batrachideidae			
Sf. Tridactyloidea			
Ripipterygidae			
Tridactylidae			
Tridactylis apicalis Say	Ferris 1942; Gangwere 1965	Costa Lima 1968	131.
Sf. Cylindroachetoidea			
Cylindrachetidae			
Cylindroryctes spegazzinii Giglio-Tos	Beier 1955	Beier 1955; [Kevan 1982a]	132.
PHASMATODEA			
So. Tinematodea			
Sf. Tinematoidea			
Tinematidae			
Timema sp.	Crampton [1916], 1923b, 1932	Milne & Milne 1980; Arnett 1985	133.
So. Phasmatoidea			
Sf. Bacilloidea			
Bacillidae			
Bacunculidae			
Anisomorpha ferruginea (Beauvois)	[Crampton 1916, 1923b]; [Littig 1942]; DuPorte 1962b	Comstock 1977; Arnett 1985	134.
Sf. Phylloidea			
Phyllidae			
Sf. Necroserioidea			
Necrosciidae			
Necrosia sparaxes Westwood	Gangrade 1965	Comstock 1977; Arnett 1985	135.

taxon	mouthpart-morphology data	dietary data	no.
Heterocnemiidae			
Diaphanaeromera femorata (Say)	Yuasa 1920; Walker 1933; Hudson 1945; DuPorte 1962b; Gangwere 1965	Fernald 1935; Milne & Milne 1980	136.
Lonchodidae			
Carausius morosus Brocher	Marquardt 1939; Scholl 1969	Comstock 1977; Arnett 1985	137.
Pachymorphidae			
Palophidae			
Sf. Phasmatoidea			
Bacteriidae			
Phasmatidae			
Phryganistria virgea (Westwood)	Strenger 1942	Comstock 1977; Arnett 1985	138.
DERMAPTERA			
So. Forficulina			
Sf. Pygidicranoidea			
Pygidicranidae			
Echinosoma afrum Beauvois	Giles 1963	Richards & Davies 1977	139.
Karschiellidae			
Diplatyidae			
Sf. Labiduroidea			
Carcinophoridae			
Anisolabis maritima (Gene)	Yuasa 1920; Crampton 1921, 1923b, [1932]; [Ferris 1942]; Dorsey 1943; DuPorte [1946], 1960b; Snodgrass 1947, 1960; Giles 1963	Pruthi 1969; Richards & Davies 1977	140.
Labiduridae			
Labidura riparia (Pallas)	Popham 1959; Kadam 1961	[Clausen 1940]; [Milne & Milne 1980]	141.
Apachyidae			
Sf. Forficuloidea			
Labiidae			
Chelisochidae			
Forficulidae			
Forficula auricularia Linneaus	Evans 1921; Snodgrass 1928, 1932, 1947; Walker 1931a, 1933; Strenger 1949; Henson 1950; Popham 1959; Moulins 1969; Richards & Davies 1977	Clausen 1940; Swan & Papp 1972	142.
So. Hemimerina			
Hemimeridae			
Hemimerus talpoides Walker	Hansen 1894; [Crampton 1923b], 1932c]; Popham 1962; Giles 1963	Rehn & Rehn 1936; Ashford 1970; Waage 1979	143.
So. Arixeniina			
Arixeniidae			
Arixenia esau Jordan	[Crampton 1921]; Popham 1962 [Giles 1963]	Marshall 1987; Waage 1979	144.

taxon	mouthpart-morphology data	dietary data	no.
EMBIOPTERA			
Clothidae			
Embiidae			
Embia ramburi Rimsky-Korsakov	[Crampton 1917, 1932]; [Walker 1931a]; Rahle 1970	[Costa Lima 1968]	145.
Notoligotomidae			
Notoligotoma hardyi (Friedericks)	Friedericks 1914; Davis 1936; Ross 1963	diet undocumented	146.
Embolychidae			
Embolyntha batesi MacLachlan	Lacombe 1958, 1964	Costa Lima 1968	147.
Anisembiidae			
Anisembia sp.	Chamberlin 1923	diet undocumented	148.
Australembiidae			
Australembia incompta Ross	[Krauss 1911]; Ross 1963	[Ross 1963]	149.
Oligotomidae			
Oligotoma hospes Myers	[Crampton 1923b]; Walker [1932];	[Richards & Davies 1977]	150.
Teratembiidae			
Teratembia geniculata Krauss	Krauss 1911; Ross 1952	[Richards & Davies 1977]	151.
PLECOPTERA			
So. **Arctoperlaria**			
Sf. **Nemouroidea**			
Nemouridae			
Nemoura varigata Olivier	[Evans 1921]; Hoke 1924	Hynes 1942	152.
*Nemoura venosa** Banks	Claassen 1931; [Moulins 1969]	Claassen 1931	153.
Notonemouridae			
*Notonemoura latipennis** McLellan	McLellan 1968	diet undocumented	154.
Capniidae			
Capnia necydaloides Newman	Crampton 1917; Hoke 1924	Borror & White 1970	155.
*Capnia vernalis** Newport	Claassen 1931; [Chisholm 1962];	Claassen 1931	156.
Leuctridae			
*Leuctra klapaleki** Kempny	Claassen 1931; [Strenger 1952]	Claassen 1931	157.
Leuctra sp.	Hoke 1924; Crampton 1932	Borror & White 1970	158.
Taeniopterygidae			
*Taeniopteryx frigidus** Hagen	Claassen 1931	Claassen 1931	159.
Taeniopteryx frigidus Hagen	Hoke 1924; [Metcalf & Flint 1932]	Newcomer 1918; Borror & White 1970	160.
Scopuridae			
Sf. **Subulipalpia**			
Perlidae			
Acroneuria abnormis Newman	Hoke 1924; [Snodgrass 1947]	Claassen 1931	161.
*Acroneuria pacifica** Banks	Claassen 1931; DuPorte 1946	Milne & Milne 1980	162.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
*Perla cephalotes** Curtis	[Crampton 1923b]; [Hoke 1924]; [Strenger 1952]; Chisholm 1962	Chisholm 1962	163.
Perla maxima (Scopoli)	[Walker 1931a]; Richards & Davies 1977	Chisholm 1962	164.
*Perlesta placida** Hagen	Claassen 1931	Claassen 1931	165.
Perlesta placida Hagen	Hoke 1924	Chisholm 1962	166.
Perlodidae			
*Perlodes tibialis** Banks	Claassen 1931	Claassen 1931	167.
Chloroperlidae			
*Alloperla minuta** Banks	Claassen 1931	Claassen 1931	168.
Alloperla minuta Banks	Hoke 1924	Richards & Davies 1977	169.
*Chloroperla cydippe** Newman	Claassen 1931	Claassen 1931	170.
Chloroperla grammatica Scopoli	Hoke 1924	Richards & Davies 1977	171.
Isopteryx tripunctata Scopoli	Hoke 1924	Claassen 1931	172.
Peltoperlidae			
Peltoperla * sp.	Claassen 1931; Crampton 1932	Claassen 1931	173.
Pteronarcyidae			
*Pteronarcys californica** Newman	Hosford 1913; Crampton 1917, 1932; [Hoke 1924]; Claassen 1931; Walker 1933; Snodgrass 1947; [Chisholm 1962]	Borror & White 1970; Milne & Milne 1980	174.
Pteronarcys regalis Newman	Comstock & Kochi 1902; Hoke 1924	Claassen 1931	175.
So. Anarctoperlaria			
Sf. Eusthenoidea			
Diamphipnoidae			
*Diamphipnoa annulata** (Brauer)	Illies 1960	[Baumann 1982]	176.
Eustheniidae			
Neuroperla schedingi Navas	Illies 1960	[Baumann 1982]	177.
Sf. Leptoperloidea			
Austroperlidae			
*Austroperla** sp.	Chisholm 1962	Tillyard 1926	178.
Austroperla sp.	Chisholm 1962	Tillyard 1926	179.
Gripopterygidae			
*Perlurgoperla personata** Illies	Illies 1963	[Richards & Davies 1977]	180.

taxon	mouthpart-morphology data	dietary data	no.
ZORAPTERA			
Zorotypidae			
Zorotypus hubbardi Caudell	Crampton 1920, [1923], 1932; [Matsuda 1956]; [Richards & Davies 1977]	Pruthi 1969	181.
PSOCOPTERA			
So. **Trogiomorpha**			
Sf. **Atropetae**			
Lepidopsocidae			
Trogiidae			
Lepinotus sp.	Weber 1938b; Symmons 1952	Smithers 1972; New 1987	182.
Psoquillidae			
Sf. **Psocatropetae**			
Psyllipsocidae			
Psyllipsocus ramburii Selys	Gurney 1943	Gurney 1943	183.
Speleketor flocki Gurney	Gurney 1943; Snodgrass 1944	Pearman 1928; Arnett 1985	184.
Prionoglaridae			
Prionoglaris latreilli (Enderlein)	Badonnel 1931; Ball 1936; Gurney 1943	Gurney 1943	185.
So. **Troctomorpha**			
Sf. **Nanopsocetae**			
Liposcelidae			
Embidopsocus sp.	Crampton 1932; [Smithers 1972]	Smithers 1972; Richards & Davies 1977	186.
Pachytroctidae			
Sphaeropsocidae			
Sf. **Amphientometae**			
Amphientomidae			
Stigmatopathus sp.	Crampton 1932; [Smithers 1972]	diet undocumented	187.
Musapsocidae			
Troctopsocidae			
Manicapsocidae			
Compsocidae			
So. **Psocomorpha**			
Sf. **Epipsocetae**			
Epipsocidae			
Dubellapsocidae			
Spurostigmatidae			
Philoneuridae			
Sf. **Caecilietae**			
Asiopsocidae			
Caeciliidae			
Caecilius maritimus Mockford	Mockford 1965; [Smithers 1972]	Mockford 1965	188.
Amphipsocidae			
Stenopsocidae			
Stenopsocus stigmaticus Imhoff & Labrum	[Badonnel 1934]; Smithers 1972; Matsuda 1965	Smithers 1972	189.
Polypsocidae			

taxon	mouthpart-morphology data	dietary data	no.
Sf. Homilopsocetae			
Elipsocidae			
Philotarsidae			
Mesopsocidae			
Rhinopsocus arduus Badonnel & Lienhard	Badonnel & Lienhard 1988	Badonnel & Lienhard 1988	190.
Lachesillidae			
Peripsocidae			
Ectopsocidae			
Ectopsocus californicus (Banks)	Weber 1938b; Snodgrass 1944	Swan & Papp 1972	191.
Hemipsocidae			
Calopsocidae			
Pseudocaeciliidae			
Trichopsocidae			
Archipsocidae			
Sf. Psocetae			
Psocidae			
Amphigerontia contaminata Stephens	Weber 1938b	New 1987	192.
Psocus confraternus Banks	[Burgess 1878]; [Berlese 1909]; Snodgrass 1928; Crampton [1923b], 1932; [Cook 1944]; [DuPorte 1946]	[Costa Lima 1968]; Arnett 1985	193.
Thrysophoridae			
Psilopsocidae			
Myopsocidae			
ANOPLURA			
Echinophthiriidae			
Enderleinellidae			
Haematopinidae			
Haematopinus suis (Linneaus)	Stojanovich 1945; Snodgrass 1947; Symmons 1952; Young 1953; Ramcke 1965; Lavoipierre 1967; James & Harwood 1969; Wirtz 1986; Chaudonneret 1989a	Swan & Papp 1972; Milne & Milne 1980	194.
Hamophthiriidae			
Hoplopleuridae			
Neohaematopinus citellinus Ferris	Stojanovich 1945	Milne & Milne 1980	195.
Hybophthiridae			
Linognathidae			
Linognathus vituli (Linneaus)	Stojanovich 1945	Swan & Papp 1972	196.
Microthoraciidae			
Neolinognathidae			
Pecaroecidae			
Pedicinidae			

taxon	mouthpart-morphology data	dietary data	no.
Pediculidae			
Pediculus humanus Linneaus	Peacock 1919; [Crampton 1923b]; Metcalf 1929; Snodgrass 1944, 1947; Stojanovich 1945	Milne & Milne 1980	197.
Polyplacidae			
Phthiridae			
Phthirus pubis Linneaus	Hirsch 1986	Arnett 1985	198.
Ratemiidae			
MALLOPHAGA			
So. **Amblycera**			
Menoponidae			
Ancistrona vagelli (Fabricius)	Snodgrass [1905], 1944; [Cummings 1912]; Symmons 1952; [Richards & Davies 1977]	Symmons 1952	199.
Colpocephalum subaequale Burmeister	Symmons 1952	Symmons 1952	200.
Myrsidea cornicis (De Geer)	[Qadri 1936]; Buckup 1959	Buckup 1959	201.
Pseudomenopon pilosum (Scopoli)	[Qadri 1936]; Haub 1967	Haub 1967	202.
Tetrophthalmus sp.	Cope 1941	[Arnett 1985]	203.
Laemobothridae			
Laemobothrion gypsis Kellogg	Snodgrass 1905; Crampton 1923b; [Qadri 1936]; [Symmons 1952]; [Richards & Davies 1977]	[Arnett 1985]	204.
Ricinidae			
Trochiloecetes sp.	Clay 1949	[Arnett 1985]	205.
Boopidae			
Heterodoxus spiniger (Enderlein)	Symmons 1952	Symmons 1952	206.
Trimenoponidae			
Trimenopon jenningsi Kellogg & Paine	Stowe 1943; Symmons 1952	[Arnett 1985]	207.
Abrocomophagidae			
Gyropidae			
Gyropus ovalis Burmeister	Symmons 1952	Symmons 1952	208.
So. **Ishnocera**			
Trichodectidae			
Bovicola caprae Gurlt	Risler 1951	Swan & Papp 1972	209.
Trichodectes canis (De Geer)	Symmons 1952	Symmons 1952	210.
Philopteridae			
Gonoides lagopi Linneaus	Symmons 1952	Symmons 1952	211.
Philopterus atratus Nitzsch	[Quadri 1936]; Symmons 1952	Symmons 1952	212.
Heptapsogasteridae			
Cuclotocephalus extraneus Carriker	Carriker 1937	Carriker 1937	213.

taxon	mouthpart-morphology data	dietary data	no.
So. Rhynchopthirina			
Haematomyzidae			
Haematomyzus elephantis Piaget	Ferris 1931; Snodgrass 1944, 1947; Symmons 1952; Mukerji & Sen-Sarma 1955; Richards & Davies 1977	Mukerji & Sen-Sarma 1955; Symmons 1952	214.
THYSANOPTERA			
So. Terebrantia			
Aeolothripidae			
Aeolothrips fasciatus Linneaus	[Jordan 1888]; Garman 1896; [Doeksen 1941]; Mickoleit 1963	Richards & Davies 1977; Mound 1986, in litt.; Kirk 1986, in litt.	215.
Melanthrips ficalbii Buffa	Doeksen 1941	Doeksen 1941	216.
Heterothripidae			
Merothripidae			
Thripidae			
Chirothrips hamatus (Trybom)	[Jordan 1888]; Jones 1954	[Costa Lima 1968]; Mound 1986, in litt.; Kirk 1986, in litt.	217.
Frankliniella tritici (Fitch)	Borden 1915; Peterson 1915	Borden 1915; Mound 1986, in litt.; Kirk 1986, in litt.	218.
Heliothrips femoralis (Reuter)	Peterson 1915; [Doeksen 1941]; [Snodgrass 1944]	[Johnson & Lyon 1976]; Mound 1986, in litt.; Kirk 1986, in litt.	219.
Thrips physapus Linneaus	[Jordan 1888]; [Muir & Kershaw 1911]; Peterson 1915; [Snodgrass 1944]; Risler 1957	Peterson 1915; Risler 1957; [Hill 1983]; Mound 1986, in litt.; Kirk 1986, in litt.	220.
So. Tubulifera			
Phlaeothripidae			
Cephalothrips yuccae Hinds	Peterson 1915	Peterson 1915; [Costa Lima 1968]; Mound 1986, in litt.; Kirk 1986, in litt.	221.
Haplothrips verbasci (Osborn)	[Doeksen 1941]; Heming 1978	[Costa Lima 1968]; Heming 1978; Mound 1986, in litt.; Kirk 1986, in litt.	222.
Phlaeothrips coriaceus Haliday	[Jordan 1888]; [Doeksen 1941]; Mickoleit 1963	Mickoleit 1963; [Costa Lima 1968]; Mound 1986, in litt.; Kirk 1986, in litt.	223.

taxon	mouthpart-morphology data	dietary data	no.
HETEROPTERA			
So. **Enicocephalomorpha**			
Sf. **Enicocephaloidea**			
Enicocephalidae			
Systelloderes biceps (Say)	Spooner 1938	Cobben 1978	224.
So. **Dipscomorpha**			
Sf. **Dipscoroidea**			
Dipscocoridae			
Pachycoleus walti Feiber	Cobben 1978	Hungerford 1919; Cobben 1978	225.
Ceratocombidae			
Ceratocombus vagans McAtee & Malloch	Spooner 1938; [Cobben 1978]	Blatchley 1926	226.
Hypsipterygidae			
*Hypsipteryx machadoi** Drake	Stys 1970	Cobben 1978; [Slater 1982]	227.
Schizopteridae			
Schizoptera stricklandi China	Cobben 1978	Blatchley 1926	228.
So. **Nepomorpha**			
Sf. **Nepoidea**			
Nepidae			
Nepa cinera Linneaus	Hamilton 1931; [Parsons 1962]; [Coppen 1978]	Riley 1918; Blatchley 1926; Milne & Milne 1980	229.
Ranatra fusca Beauvois	Neiswander 1926; Parsons 1966	Riley 1918; Blatchley 1926	230.
Belostomatidae			
Belostoma indicus LePeletier & Servadei	[Berlese 1909]; Crampton 1921; Qadri 1951; Verma, Tyagi & Gupta 1973	Blatchley 1926	231.
Benacius griseus (Say)	Meinert 1897; Butt 1943; [Parsons 1963, 1964, 1966]	Uhler 1884; Milne & Milne 1980	232.
Sf. **Corixoidea**			
Corixidae			
Corixa punctata Illiger	Banks 1939; Benwitz 1956; Gouin 1968; [Cobben 1978]	Milne & Milne 1980	233.
Hesperocorixa interrupta (Say)	Marks 1957; Parsons 1966a, 1966b	Swan & Papp 1972	234.
Sf. **Gelastocoroidea**			
Gelastocoridae			
Gelastocoris oculatus (Fabricius)	Weber 1930; [Spooner 1938]; Parsons 1958a, 1958b, 1959, 1962, 1965, 1966a, 1966b; [Gouin 1968]; [Cobben 1978]	Blatchley 1926; Milne & Milne 1980	235.
Ochteridae			
Ochterus americanus (Uhler)	Spooner 1938; Parsons 1965; [Denis & Bitsch 1973]; [Rieger 1976]; [Cobben 1978]	Uhler 1884; Blatchley 1926	236.
Sf. **Naucoroidea**			
Naucoridae			
Ambrysus magnaceps La Rivers	Parsons 1966a, 1966b; [Denis & Bitsch 1973]	Richards & Davies 1977	237.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
Naucoris cimicoides Linneaus	Bekker 1929	Richards & Davis 1977	238.
Aphelocheiridae			
Apheliocheirus aestivalis Fabricius	Parsons 1966b, 1969; [Cobben 1978]	Richards & Davies 1977	239.
Sf. Notonectoidea			
Notonectidae			
Notonecta glauca Linneaus	Weber 1930; [Butt 1943]; [Marks 1957]; [Snodgrass 1960]; [Parsons 1965, 1966, 1972]; [Denis & Bitsch 1973]; [Cobben 1978]	Poulton 1906; Swan & Papp 1972; Milne & Milne 1980	240.
Pleidae			
Plea atomaria Palisot de Beauvois	Weber 1930; Cobben 1978	[Blatchley 1926]	241.
Helotrephidae			
Neotrephes usingeri China	China 1936	China 1936; [Slater 1982]	242.
So. Gerromorpha			
Mesoveliidae			
Mesovelia mulsanti White	Cobben 1978	[Swan & Papp 1972]	243.
Hydrometridae			
Hydrometra stagnorum Linneaus	[Ekblom 1926]; Servadei 1946; Cobben 1978	[Blatchley 1926]	244.
Hebridae			
Hebrus ruficeps Thomas	Cobben 1978	[Swan & Papp 1972]	245.
Paraphrynoveliidae			
Paraphrynovelia brincki Poisson	Anderson 1978	Anderson 1978	246.
Macroveliidae			
Veliidae			
Microvelia reticulata Burmeister	Cobben 1978	Blatchley 1926	247.
Velia rivulorum Fabricius	Meinert 1897; [Ekblom 1926]; Servadei 1946; Cobben 1978	Blatchley 1926	248.
Madeoveliidae			
Gerridae			
Gerris najas De Geer	Meinert 1897; [Ekblom 1926]; [Weber 1930]; [Spooner 1938]; Servadai 1946; Brinkhurst 1960; [Parsons 1962, 1965, 1966]; [Cobben 1978]	Milne & Milne 1980	249.
Hermatobatidae			
Hermatobates weddi China	China 1957; Anderson & Polhemus 1976	Anderson & Polhemus 1976; [Richards & Davies 1977]	250.
So. Leptopodomorpha			
Omaniidae			
Omania coleoptrata Torváth	Cobben 1970, 1978	Cobben 1970	251.
Saldidae			
Pentacora sp.	Spooner 1938; [Cobben 1978]; Hamilton 1981	Blatchley 1926	252.
Saldula pallipes Fabricius	[Ekblom 1926]; Parsons 1962, 1965; Cobben 1978	[Blatchley 1926]; [Hungerford 1919]	253.

taxon	mouthpart-morphology data	dietary data	no.
Leotichiidae			
Leotichius glaucopis Distant	China 1933; [Cobben 1978]	China 1933; [Slater 1982]	254.
Leptopodidae			
Leptopus marmoratus Goeze	China 1933; [Cobben 1978]	China 1933; [Slater 1982]	255.
So. Cimicomorpha			
Thaumastocoridae			
Joppeicidae			
Joppeicus paradoxus Puton	China 1955; Davis & Usinger 1970	China 1955; Davis & Usinger 1970; [Slater 1982]	256.
Sf. Tingoidea			
Tingidae			
Corythuca ciliata Say	Spooner 1938	Arnett 1985	257.
Tingis buddleiae Drake	[Drake & Davis 1959]; Livingstone 1969	Livingstone 1969	258.
Vianaididae			
Anommatocoris coleoptratus (Kormilev)	Drake & Davis 1959	Davis & Davis 1960; [Slater 1982	259.
Sf. Miroidea			
Miridae			
Adelphocoris rapidis (Say)	Spooner 1938	Milne & Milne 1980	260.
Lygus pabulinus Linneaus	Awati 1914; Cobben 1978	Hill 1983	261.
Miris dolobratus (Linneaus)	Spooner 1938	Blatchley 1926	262.
Microphysidae			
Loricula elegantula (Baerenspring)	Cobben 1978	[Cobben 1978]	263.
Sf. Cimicoidea			
Velocipedidae			
Medocostidae			
Medocostes lestoni Stys	Stys 1967	Stys 1967	264.
Nabidae			
Nabis subcoleopteratus Kirby	[Ekblom 1926]; Spooner 1938; [Cobben 1978]	[Poulton 1906]; Milne & Milne 1980	265.
Plokiophilidae			
Plokiophiloides biforis Carayon	Carayon 1974	Carayon 1974	266.
Anthocoridae			
Triphleps insidiosa (Say)	Spooner 1938	[Cobben 1978]	267.
Cimicidae			
Cimex lectularius Linneaus	Kemper 1932; Snodgrass 1944; Dickerson & Lavoipierre 1959; Cobben 1978	Edwards 1960	268.
Polyctenidae			
Hesperoctenes cartus Jordan	Ferris & Usinger 1939	Ferris & Usinger 1939	269.
Sf. Reduvoidea			
Pachynomidae			
Reduviidae			
Reduvius personatus (Linneaus)	Weber 1930; Snodgrass 1944; Cobben 1978	Blatchley 1926	270.

taxon	mouthpart-morphology data	dietary data	no.
Rhodnius prolixus (Stal)	Lavoipierre, Dickerson & Gordon 1959; James & Harwood 1969; [Cobben 1978]; Smith 1985; Wirtz 1987	Milne & Milne 1980; Smith 1985	271.
Triatoma infestans (Klug)	Snodgrass 1944; Barth 1952	Edwards 1961; [Blatchley 1926]	272.
So. Pentatomomorpha			
Sf. Aradoidea			
Aradidae			
Aradus sp.	Spooner 1920; China 1931; Weber 1930; [Stys 1969]; [Cobben 1978]	Blatchley 1926; [China 1931]; [Cobben 1978]	273.
Termitaphididae			
Termititaradus panamensis Myers	Myers 1924; China 1931	Myers 1924; [China 1931]	274.
Idiostolidae			
Idiostolus insularis Berg	Scudder 1962	Scudder 1962	275.
Piesmatidae			
Piesma cinerea (Say)	Spooner 1938; Drake and Davis 1958; [Cobben 1978]	Drake & Davis 1958; Cobben 1978	276.
Colobathristidae			
Berytidae			
Jalysus spinosus (Say)	Spooner 1938	Elsey & Stinner 1971; Cobben 1978	277.
Neides muticus (Say)	Spooner 1938; [Cobben 1978]	Cobben 1978	278.
Malcidae			
Lygaeidae			
Oncopeltus fasciatus (Dallas)	Snodgrass 1947; Forbes 1976; Cobben 1978; Smith 1985; Bolender & Honomichl 1985	Blatchley 1926; Milne & Milne 1980	279.
Pyrrhocoridae			
Dysdercus cingulatus Fabricius	[MacGill 1947]; [Kumari 1955]; Rathore 1961; [Popham 1962]; [Saxena 1963]; [Khan 1972]; [Cobben 1978]	Hill 1983	280.
Pyrrhocoris apterus (Linneaus)	Wedde 1885; Bugnion & Popoff 1911; Cobben 1978	Hill 1983; Cobben 1978	281.
Largidae			
Sf. Coreoidea			
Stenocephalidae			
Hyocephalidae			
Hyocephalus apragnus Bergroth	Stys 1964	Stys 1964; [Slater 1982]	282.
Coreidae			
Anasa tristis (De Geer)	Tower 1913, 1914; Metcalf, Flint & Metcalf 1962; Cobben 1978	Blatchley 1926; Milne & Milne 1980	283.
Leptocorisa varicornis Fabricius	Akbar 1957	Richards & Davies 1977; Hill 1983	284.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
Alydidae			
Alydus sp.	Spooner 1938	[Cobben 1978]	285.
Rhopalidae			
Sf. Pentatomoidea			
Thaumastellidae			
Urostylidae			
Plataspidae			
Coptosomoides myrmecophilus China	China 1931	China 1931	286.
Aphylidae			
Lestoniidae			
Cydnidae			
Cyrtomenus mirabilis (Perty)	Spooner 1938	[Cobben 1978]	287.
Thyreocoridae			
Megarididae			
Canopidae			
Canopus sp.	McAtee & Malloch 1928	[Richards & Davis 1977]	288.
Scutelleridae			
Stethaulax marmoratus (Say)	Spooner 1938	[Cobben 1978]	289.
Tessaratomidae			
Tessaratoma papillosa	Bugnion & Popoff 1911	Hill 1983	290.
Eumenotidae			
Dinidoridae			
Coridius janus (Fabricius)	Banerji 1960; Rastogi 1965	Banerji 1960; Rastogi 1965	291.
Pentatotomidae			
Graphosoma lineatus (Linneaus)	Bugnion & Popoff 1911; [Weber 1930]; Cobben 1978	Weber 1930	292.
Palomena prasina Linneaus	Weber 1930	Weber 1930	293.
Acanthosomatidae			
Phloeidae			
HOMOPTERA			
So. Coelorrhyncha			
Peloridiidae			
Hemiodoecus leai China	[Evans 1937]; Singh 1971; [Hamilton 1981]; Bourgoin 1986a, 1986b	[Johnson & Lyon 1976]; [Richards & Davies 1977]	294.
So. Auchenorrhyncha			
Sf. Fulgoroidea			
Cixiidae			
Cixius pini Fitch	Spooner 1938; [Hamilton 1981]; [Bourgoin 1986a]	[Johnson & Lyon 1976]	295.
Oliarus vicarius (Walker)	Spooner 1938	[Johnson & Lyon 1976]	296.
Tettigometridae			
Phalix titan Fennah	Fennah 1952; [Bourgoin 1986a, 1986b]	[Kosztarab 1982]	297.
Delphacidae			
Pentagramma vittatifrons (Uhler)	Snodgrass 1938; Spooner 1938	[Johnson & Lyon 1976]	298.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
Eubrachyidae			
Eurybrachys sp.	Chatterjee 1933; Bourgoin 1986b	Chatterjee 1933	299.
Fulgoridae			
Cyropotus reineckei Van Duzee	Spooner 1938	[Johnson & Lyon 1976]	300.
Melicharia quadrata Kirby	Singh 1971	[Johnson & Lyon 1976]	301.
Achilidae			
Catonia nava (Say)	[Spooner 1938]; Snodgrass 1947	Arnett 1985	302.
Tropiduchidae			
Pelitropis rotatula Van Duzee	Spooner 1938	[Johnson & Lyon 1976]	303.
Issidae			
Bruchomorpha sp.	Spooner 1938	[Johnson & Lyon 1976]	304.
Lophopidae			
Pyrilla perpusilla Walker	Qadri & Aziz 1950	Qadri & Aziz 1950	305.
Acanaloniidae			
Acanalonia latifrons (Walker)	Spooner 1938	[Johnson & Lyon 1976]	306.
Ricaniidae			
Flatidae			
Cyarda melichari Van Duzee	Spooner 1938	[Johnson & Lyon 1976]	307.
Flata sp.	Muir & Kershaw 1912	[Johnson & Lyon 1976]	308.
Derbidae			
Amaloptera uhleri Van Duzee	Spooner 1938	[Johnson & Lyon 1976]	309.
Otiocerus degeeri Kirby	Spooner 1938	[Johnson & Lyon 1976]	310.
Achilixiidae			
Meenoplidae			
Kinnaridae			
Dictyopharidae			
Dictyophara florens (Stal)	Spooner 1938; [Bourgoin 1986a]	[Johnson & Lyon 1976]	311.
Scolops pungens Germar	Kramer 1950; Evans 1973; [Bour- 1986b]	[Swan & Papp 1972]	312.
Gengidae			
Nogodinidae			
Bladina synavei Kramer	Fennah 1952; Kramer 1976	Kramer 1976	313.
Hypochthonellidae			
Hypochthonella caeca China & Fennah	China & Fennah 1952; Bourgoin 1986a	China & Fennah 1952	314.
Sf. Cercopoidea			
Cercopidae			
Cephiscus siccifolius (Walker)	Snodgrass 1938; Butt 1943	Costa Lima 1968	315.
Lepyronia quadrangularis (Say)	Spooner 1938; Kramer 1950	[Swan & Papp 1972]	316.

taxon	mouthpart-morphology data	dietary data	no.
Sf. **Cicadoidea**			
Cicadidae			
Magicicada septendecem (Linneaus)	Meek 1903; [Berlese 1909]; [Crampton 1921c]; Snodgrass 1921, 1928, 1935, 1944, 1947, 1950; Murti 1929; Butt 1943; Kramer 1950	Swan & Papp 1972; Dybas & Lloyd 1974; Milne & Milne 1980; Young 1984	317.
Sf. **Cicadelloidea**			
Cicadellidae			
Aulacizes irrorata Fabricius	Kramer 1950	Costa Lima 1968	318.
Idiocerus atkinsoni Lethierry	[Qadri 1949]; Arora & Singh 1962; [Tribout 1956]	Pruthi 1969	319.
Typhlocyba ulmi Linneaus	Willis 1949	Willis 1949	320.
Wolfella caternaulti Spinola	Evans 1975	[Kosztarab 1982]	321.
Sf. **Membracoidea**			
Membracidae			
Entylia sinuata Fabricius	Branch 1913; [Hamilton 1981]	Branch 1913	322.
Eurymeloides pulcra Signoret	Evans 1937	[Richards & Davies 1977]	323.
Stictocephala bulbalus (Fabricius)	Kramer 1950	Johnson & Lyon 1976	324.
Aetalionidae			
Dorthula hardwickii Gray	Evans 1975	[Kosztarab 1982]	325.
Biturritiidae			
Melizoderes darwini Funkhouser	Evans 1975	[Kosztarab 1982]	326.
Nicomiidae			
So. **Sternorrhyncha**			
Sf. **Psylloidea**			
Psyllidae			
Psylla mali Schmidberger	Grove 1919; Weber 1928, 1929, 1930; [Forbes 1972]; [Smith 1985]	Swan & Papp 1972; Milne & Milne 1980	327.
Sf. **Aleyrodoidea**			
Aleyrodidae			
Trialeurodes vaporariorum (Westwood)	Hargreaves 1915; Weber 1928, 1930; [Spooner 1938]; Forbes 1972	Costa Lima 1968; Swan & Papp 1972; Milne & Milne 1980	328.
Sf. **Aphidoidea**			
Aphididae			
Aphis fabae Linneaus	Weber 1928; [Forbes 1977]	Swan & Papp 1972; Pollard 1973; Lawton 1976	329.
Eriosoma lanigera (Hausmann)	Davidson 1914; Herriot 1934	Costa Lima 1968; Milne & Milne 1980	330.
Myzus persicae (Sulzer)	Forbes 1969, 1977	Pollard 1973; Johnson & Lyon 1976	331.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
Adelgidae			
*Cnaphalodes strobilobius** Kaltenbach	Speyer 1923	Speyer 1923	332.
Phylloxeridae			
*Phylloxera vitifoliae** Fitch	[Duncan 1922]; Maillet 1957	Maillet 1957; Johnson & Lyon 1976	333.
Sf. Coccoidea			
If. Archaeococcoidea			
Ortheziidae			
Orthezia urticae Linneaus	Balachowsky 1937; [Jancke 1955]	Borror, DeLong & Triplehorn 1976; Arnett 1985	334.
Margarodidae			
Icerya purchasi Maskell	Balachowski 1937	Borror, DeLong & Triplehorn 1976; Arnett 1985	335.
Margarodes vitium Giard	[Jancke 1955]; Theron 1958	Borror, DeLong & Triplehorn 1976; Arnett 1985	336.
Matsuococcus bisetosus Morrison	[Weber 1930]; Beardsley 1968	Borror, DeLong & Triplehorn 1976; Arnett 1985	337.
Phenacoleachiidae			
Phenacoleachis zelandica (Maskell)	Jancke 1955; [Theron 1968]	Borror, DeLong & Triplehorn 1976; Arnett 1985	338.
If. Neococcoidea			
Stictococcidae			
*Stictococcus multispinosus** Newstead	Richard 1971	Richard 1971	339.
Putoidae			
Pseudococcidae			
*Pseudococcus adonidum** (Linneaus)	Weber 1928, 1930; [Jancke 1955]; [Theron 1958]; [Giliomee 1961]	Lowe 1898; Pirone 1970; Hill 1983	340.
Coccidae			
Coccus hesperidium Linneaus	[Jancke 1955]; Giliomee 1967a	Borror, DeLong & Triplehorn 1976; Arnett 1985	341.
Eulecanium tiliae (Linneaus)	Balachowsky 1937; [Theron 1958];	Borror, DeLong & Triplehorn 1976; Arnett 1985	342.
Physokermes piceae (Schrank)	Jancke 1955; Giliomee 1967a	Borror, DeLong & Triplehorn 1976; Arnett 1985	343.
Aclerdidae			
Dactyloppidae			
Dactylopius austrinus De Lotto	De Lotto 1974	De Lotto 1974	344.
Kermesidae			
Kermes quercus Linneaus	Jancke 1955	Borror, DeLong & Triplehorn 1976	345.
Cryptococcidae			
Eriococcidae			
Acanthococcus granulatus Griswold	Jancke 1955	Borror, DeLong & Triplehorn 1976; Arnett 1985	346.

taxon	mouthpart-morphology data	dietary data	no.
Apiomorphidae			
Apiomorpha ?pharetrata (Schrader)	Theron 1968	Borror, DeLong & Triplehorn 1976	347.
Kerridae			
*Laccifer lacca** Kerr	Stebbing 1910; Imms & Chatterjee 1915; Balachowsky 1937	Richards & Davies 1977	348.
Beesoniidae			
*Beesonia dipterocarpi** Green	Green 1926	Green 1926	349.
Lecanodiaspididae			
Lecaniodiaspus elytropappi Munting & Giliomee	[Ferris 1955]; Giliomee 1967b, 1968	Borror, DeLong & Triplehorn 1976; Arnett 1985	350.
Cerococcidae			
Asterolecaniidae			
Asterolecanium ungulatum Russell	Russell 1941; [Jancke 1955]; [Giliomee 1968]	Borror, DeLong & Triplehorn 1976; Arnett 1985	351.
Conchaspididae			
Conchaspis vayssieri Mamet	Mamet 1954	Mamet 1954	352.
Phoenicococcidae			
Halimococcidae			
*Palmaricococcus nesiotes** (Laing)	Zimmerman 1948	diet undocumented	353.
Diaspididae			
Parlatoria blanchardi Targioni-Tozetti	[Weber 1930]; Balachowsky 1937	Arnett 1985	354.
Quadraspidiotus perniciosus Comstock	Jancke 1955	Borror, DeLong & Triplehorn 1976; Arnett 1985	355.
MEGALOPTERA			
Corydalidae			
Chauliodes formosanus Pictet	[Crampton 1921c]; Maki 1936;	[Milne & Milne 1980]	356.
*Chauliodes formosanus** Pictet	Maki 1936; [Snodgrass 1960]	[Milne & Milne 1980]	357.
Corydalus cornutus (Linneaus)	Packard 1898; Comstock & Kochi 1902; Kellogg 1902; [Crampton 1923b]; Rober 1941; Dorsey 1943; Kelsey 1954; Kramer 1955	Swan & Papp 1972; Milne & Milne 1980	358.
*Corydalus cornutus** (Linneaus)	Kellogg 1902; [Hosford 1913]; Snodgrass 1935, 1960; Cook 1944a; DuPorte 1946; Kramer 1955	Swan & Papp 1972; [Borror, DeLong & Triplehorn 1976]	359.
Neohermes sp.	Ferris 1942; Cook 1943	[Borror, DeLong & Triplehorn 1976]	360.
Sialidae			
Sialis flavilatera (Linneaus)	[Smith 1898]; [Crampton 1921c, 1932]; Rober 1941	[Swan & Papp 1972]; Arnett 1985	361.
Sialis lutaria * Linneaus	[Crampton 1921c, 1923b]; Evans 1921; Das 1938; [Rober 1941]	[Swan & Papp 1972]; Richards & Davies 1977	362.

taxon	mouthpart-morphology data	dietary data	no.
RAPHIDIOPTERA			
Raphidiidae			
Aquilla admixa (Hagen)	Ferris & Pennebaker 1939; Matsuda 1956	[Swan & Papp 1972]; [Milne & Milne 1980	363.
Raphidia flavipes Stein	[Evans 1921]; Achtelig 1967	Clausen 1940; Arnett 1985	364.
*Raphidia** sp.	Crampton 1917b, 1921c; Das 1938; Snodgrass 1947; [Genay 1953]; Hinton 1963	Clausen 1940; [Richards & Davies 1977]	365.
Inocellidae			
PLANIPENNIA			
Sf. Ithonoidea			
Ithonidae			
*Ithone fusca** Newman	Crampton 1921c; Tillyard 1923	Clausen 1940; [Arnett 1985]	366.
Polystoechotidae			
Polystoechotes sp.	Crampton 1921c; [Ferris 1942]	[Borror, DeLong & Triplehorn 1976]	367.
Sf. Coniopterygoidea			
Coniopterygidae			
*Aleuropteryx loewi** Klapalek	Rousset 1966	[Clausen 1940]; [Richards & Davies 1977]	368.
*Coniopteryx pygmaea** Enderlein	Withycombe 1922; Genay 1953; Rousset 1956, 1958, 1966	[Clausen 1940]; Swan & Papp 1972	369.
Conwentzia hageni Banks	Crampton 1921c	[Arnett 1985]	370.
*Conwentzia psociformis** (Curtis)	Withycombe 1922; Rousset 1966	[Clausen 1940]; [Richards & Davies 1977]	371.
*Semidalis aleurodiformis** Stephens	Withycombe 1922; Rousset 1966	[Clausen 1940]; [Richards & Davies 1977]	372.
Sf. Mantispoidea			
Dilaridae			
*Nailachius americanus** (MacLachlan)	Gurney 1947	[Borror, DeLong & Triplehorn 1976]; [Arnett 1985]	373.
Berothidae			
*Lomamyia latipennis** Carpenter	[Gurney 1947]; Tauber & Tauber 1968	[Borror, DeLong & Triplehorn 1976]; [Arnett 1985]	374.
Mantispidae			
Mantispa pagana	[Packard 1898]; [Crampton 1921c, 1932; [DuPorte 1946b]; [Ross 1982]	[Clausen 1940]; Borror, DeLong & Triplehorn 1976	375.
Plega signata (Hagen)	Ferris 1940	[Borror, DeLong & Triplehorn 1976]; [Arnett 1985]	376.

taxon	mouthpart-morphology data	dietary data	no.
Sf. **Osmyloidea**			
Neurorthidae			
*Neurorthus fallax** (Rambur)	Zwick 1967	Zwick 1967	377.
Osmylidae			
*Osmylus chrysops** Linneaus	[Crampton 1921c]; Withycombe	[Clausen 1940]; Arnett 1985	378.
Sisyridae			
*Climacea**	Crampton 1921c; Withycombe 1924; Brown 1952	[Richards & Davies 1977]; [Arnett 1985]	379.
Sisyra umbrata Needham	Anthony 1902; [Crampton 1921c]; Withycombe 1922, 1924	[Borror, DeLong & Triplehorn 1976]	380.
Sf. **Hemerobioidea**			
Hemerobiidae			
*Hemerobius** sp.	Evans 1921; Witycombe 1922; Snodgrass 1947; [Genay 1953]	Swan & Papp 1972; Milne & Milne 1980	381.
Psectra dipterum (Burmeister)	Crampton 1921c; Killington 1936	[Arnett 1985]	382.
Wesmaelius quadrifasciatus (Reuter)	Killington 1936	Killington 1936	383.
Chrysopidae			
Chrysopa perla Linneaus	[Metcalf 1929]; [Crampton 1921c]; [Morse 1931]; [Miller 1933]; [Hoyt 1952]; [Principi 1954]	Milne & Milne 1980	384.
*Chrysopa** sp.	Withycombe 1922, 1924; Hoyt 1952; Principi 1954; Rousset 1966	Swan & Papp 1972; [Richards & Davies 1977]	385.
Sf. **Myrmeleontoidea**			
Psychopsidae			
*Psychopsis elegans**	Crampton 1921c; Withycombe 1924	Clausen 1940	386.
Nemopteridae			
*Croce filipennis** Westwood	Withycombe 1923; Imms 1911	Imms 1911	387.
Nemoptera sinuata	Crampton 1917b, 1921a, 1923b	[Arnett 1985]	388.
Nemopterella sp.	Acker 1958	[Arnett 1985]	389.
Palmipenna aeoleoptera Picker	Picker 1987	Picker 1987	390.
Stenorrhachus walkeri MacLachlan	Hoyt 1952; Acker 1958	[Arnett 1985]	391.
Nymphidae			
Nymphes sp.	Crampton 1921c	[Clausen 1940]	392.
Ascalaphidae			
Ascalaphus libelluloides Schaeffer	Dezaly 1960	[Richards & Davies 1977]	393.
*Ascalaphus** sp.	[Crampton 1921c]; Withycombe 1924	Withycombe 1924	394.
Stilbopterygidae			
Stilbopteryx sp.	Crampton 1921c; Kimmins 1940; Riek 1968	diet undocumented	395.

taxon	mouthpart-morphology data	dietary data	no.
Myrmeleontidae			
Myrmeleon europaeus Linneaus	[Packard 1898]; [Snodgrass 1935]; Sundermeier 1940; Korn 1943	McClure 1983; Arnett 1985	396.
*Myrmeleon formicarius** Linneaus	[Dewitz 1882]; Lozinski 1908; [Sundermeier 1940]; [Korn 1943]; [Snodgrass 1947]; [Romoser 1973]	[Clausen 1940]; Griffiths 1980; Milne & Milne 1980; McClure 1983	397.
COLEOPTERA			
So. **Archostemmata**			
Ommatidae			
Cupedidae			
Cupes sp.	Pauly 1915; Stickney 1923	Crowson 1981	398.
Micromalthidae			
Micromalthus debilis LeConte	Stickney 1923; Crowson 1981	Crowson 1981	399.
So. **Myxophaga**			
Lepiceridae			
Torridincolidae			
Torridincola rhodesica Steffan	Steffan 1964	Lawrence 1982	400.
Sphaeriidae			
Sphaerius politus Horn	Stickney 1923; Crowson 1981	Crowson 1981	401.
Hydroscaphidae			
*Hydroscapha natans** LeConte	Böving & Craighead 1931; Arnett 1963; Merrit & Cummins 1984	Merritt & Cummins 1984; McCafferty & Provonsha 1983	402.
So. **Adephaga**			
Rhysodidae			
Clinidium mexicanum Chevrolat	Pauly 1915	Balduf 1935; [Pruthi 1969]	403.
Omoglymmus americanus Laporte	Pauly 1915; Stickney 1923	Evans & Forsythe 1985	404.
Carabidae			
Amara sp.	[Pauly 1915]; Dorsey 1943; [Zhavoronkova 1969]; [Evans & & Forsythe 1985]	Richards & Davies 1977; Hengeveld 1981; Crowson 1981; Forsythe 1982	405.
*Badister** sp.	Ghilarov 1964	Richards & Davies 1977	406.
Calosoma inquisitor Linneaus	[Pauly 1915]; [Stickney 1923];	[Milne & Milne 1980]	407.
*Calosoma sycophanta** Linneaus	Peterson 1951	Peterson 1951	408.
Carabus auronitens	[Kadic 1902]; Bugnion 1920; [Golden 1925]; [Zhavoronkova 1969]; [Forsythe 1982]	[Milne & Milne 1980]	409.
*Carabus** sp.	Das 1938; Richards & Davies 1977	Clausen 1940; Crowson 1981	410.

taxon	mouthpart-morphology data	dietary data	no.
Cicindela campestris Linneaus	[Berlese 1909]; [Pauly 1915]; [Williams 1938]; [Cook 1943]; [Pearson & Mury 1979]; Forsythe 1983; Evans & Forsythe 1985	Milne & Milne 1980	411.
*Cicindela hirticollis** Say	Anderson 1936; Peterson 1951; Steinmann & Zombori 1984	Milne & Milne 1980	412.
Cychrus sp.	Pauly 1915; Forsythe 1982	Forsythe 1982; Evans & Forsythe 1985	413.
Drypta sp.	Evans & Forsythe 1985	Evans & Forsythe 1985	414.
Harpalus calignosus (Fabricius)	Smith 1898; [Pauly 1915]; Crampton 1921, 1932; Dorsey 1943; [Evans 1965c]; [Zhavoronkova 1969]	Crowson 1981; [Forsythe 1982]	415.
*Harpalus** sp.	Anderson 1936; Peterson 1951; Striganova 1967	Peterson 1951	416.
Loricera pilicornis (Fabricius)	Pauly 1915; Forsythe 1982	Home 1976; Hengeveld 1981; Crowson 1981; Forsythe 1982	417.
*Loricera** sp.	Schiodte 1861/1883; Richards & Davies 1977; [Bauer & Kredler 1988]	Peterson 1951; [Bauer & Kredler 1988]	418.
Megacephala klugi Cuaudonneret	Pauly 1915; Crowson 1981	[Balduf 1935]	419.
Nebria brevicollis (Fabricius)	[Berlese 1909]; Pauly 1915; Evans 1965b, 1965c; [Rudolph 1970]; [Forsythe 1982]	Williams 1959; Evans 1965a; Hengeveld 1981; Crowson 1981; [Forsythe 1982]	420.
*Nebria** sp.	[Berlese 1909]; Pauly 1915; Evans 1965b, 1965c; [Rudolph 1970]; [Forsythe 1982]	Williams 1959; Evans 1965a; Hengeveld 1981; Crowson 1981; [Forsythe 1982]	421.
Paussus sp.	Berlese 1909; Pauly 1915; Williams 1938; Crowson 1981	Crowson 1981	422.
Pterostichus madidus (Fabricius)	Evans 1965c; [Witzke 1973]; [Forsythe 1982]; Evans & Forsythe 1985]	Milne & Milne 1980; Crowson 1981; [Hengeveld 1981]; Forsythe 1982	423.
*Scarites** sp.	Snodgrass 1928, 1935, 1960; Bitsch 1966	Pruthi 1969	424.
Stomis pumicatus (Panzer)	Forsythe 1983	Forsythe 1983	425.

taxon	mouthpart-morphology data	dietary data	no.
Tetrarcha sp.	[Stickney 1923]; Cook 1943	Milne & Milne 1980	426.
Trechus quadristriatus (Schrank)	[Pauly 1915]; [Jeannel 1960]; Forsythe 1983	Crowson 1981	427.
Tricondylia aptera Olivier	Pauly 1915	Balduf 1935	428.
Haliplidae			
*Brychius** sp.	Jaboulet 1960	Merritt & Cummins 1984	429.
*Haliplus** sp.	Peterson 1951; Jaboulet 1960; Bitsch 1966	Crowson 1981; Merritt & Cummins 1984	430.
Peltodytes duodecimpunctatus	[Pauly 1915]; Stickney 1923; McCafferty & Provoshna 1984	McCafferty & Provonsha 1983	431.
*Peltodytes** sp.	Peterson 1951; Jaboulet 1960;	Crowson 1981; Merritt & Cummins 1984	432.
Amphizoidae			
Amphizoa probably *insolens* LeConte	Pauly 1915; [Stickney 1923]; Williams 1938	Merritt & Cummins 1984	433.
Hygrobiidae			
Pelobia tardus Herbst	Pauly 1915; Balfour-Browne 1922	Balfour-Browne 1922	434.
Noteridae			
*Hydrocanthus ?iridicolor** Say	Peterson 1951; [Richards & Davies 1977]; McCafferty & Provoshna 1984	Peterson 1951; McCafferty & Provoshna 1984	435.
Dytiscidae			
Colymbetes sculptilis Harris	Williams 1938; McCafferty & Provoshna 1984	Crowson 1981; Merritt & Cummins 1984	436.
*Cybister fimbriolatus** Say	Peterson 1951; [DeMarzo 1977a, 1979]	Peterson 1951	437.
Dytiscus circumcinctus Ahrens	[Berlese 1909]; Pauly 1915; Golden 1925; Richards & Davies 1977; [Crowson 1981]	Milne & Milne 1980; [Crowson 1981]	438.
*Dytiscus** sp.	Burgess 1881; Berlese 1909; [Blunck 1916, 1918]; Korschelt 1924; Anderson 1936; Snodgrass 1947; Peterson 1951; [DeMarzo 1977a, 1979]	Milne & Milne 1980	439.
*Hyphydrus aubei** Ganglbauer	DeMarzo 1977b, 1978, 1979	[Lawrence 1982]	440.
*Laccophilus testaceus** Aube	DeMarzo 1976b, 1978	[Lawrence 1982]	441.
*Oreodytes rivalis** Gyllenhal	DeMarzo 1976b, 1977b, 1978, 1979	[Lawrence 1982]	442.

taxon	mouthpart-morphology data	dietary data	no.
Gyrinidae			
Dineutes discolor Aube	Pauly 1915; [Stickney 1923]; [Williams 1939]; Dorsey 1943	Milne & Milne 1980; Merritt & Cummins 1984	443.
*Dineutes** sp.	Anderson 1936; Dorsey 1943; Peterson 1951	Milne & Milne 1980; Merritt & Cummins 1984	444.
Gyrinus substriatus Stephens	[Pauly 1915]; Honomichl 1975	[Poulton 1906]; Merritt & Cummins 1984	445.
*Orechtochilus villosus** Muller	Noars 1956; Bitsch 1966	Clausen 1940	446.
So. Polyphaga			
Sf. Staphylinoidea			
Hydraenidae			
*Ochetibius impressus** Marsham	Bøving & Craighead 1931; Peterson 1951; Arnett 1963	Merritt & Cummins 1984	447.
Ptiliidae			
Cephaloplectus mus Mann	Seevers & Dybas 1943	Seevers & Dybas 1943	448.
Agyrtidae			
Leiodidae			
*Anisotoma blanchardi** Horn	Bøving & Craighead 1931; Lawrence 1977; Lawrence & Newton 1980	Crowson 1981	449.
Cainosternum imbricatum Notman	Wheeler 1986	Wheeler 1986	450.
*Speophyes lucidulus** (Delarouzee)	Feiffe 1965; Corbière 1967	[Borror, DeLong & Triplehorn 1976	451.
Leptinidae			
Leptinus testaceus Muller	Stickney 1923; [Crampton 1923b, 1932]; Williams 1938	Crowson 1981	452.
Platypsyllidae			
Platypsyllus sp.	[Stickney 1923]; Crampton 1923b, 1932; [Williams 1938]	Medvedev & Vysotzkaya 1969; Arnett & Jacques 1981	453.
Scydmaenidae			
*Scydmaenus tarsatus** Muller	Meinert 1888	Meinert 1888; Crowson 1981	454.
Micropeplidae			
Dasyceridae			
Silphidae			
Necrophorous sp.	Crampton 1921c; [Stickney 1923]	Milne & Milne 1980; Crowson 1981; Peschke *et. al.* 1987	455.
Silpha americana Linneaus	Williams 1938; Dorsey 1943; DuPorte 1962c; Richards & Davies 1977	Milne & Milne 1980; Arnett & Jacques 1981; [Peschke *et al.* 1987	456.
Silpha noveboracensis Forster	[Snodgrass 1928, 1935, 1960]; [Anderson 1936]; Lengerken 1938; [Dorsey 1943]; [Bitsch 1966]; Peterson 1951	Milne & Milne 1980; Arnett & Jacques 1981; [Peschke *et al.* 1987	457.

taxon	mouthpart-morphology data	dietary data	no.
*Thanatophilus** sp.	[Crampton 1921c]; Das 1938; [Lengerken 1938]	Lengerken 1938; Peschke et *al.* 1987	458.
Staphylinidae			
Agaricochara laevicollis Kraatz	Ashe 1984b	Ashe 1984a, 1984b	459.
Brachida exigua Heer	Ashe 1984b	Ashe 1984a, 1984b	460.
Brachychara probably *crassa* Sharp	Ashe 1984b	Ashe 1984a, 1984b	461.
Creophilus villosus Gravenhorst	Stickney 1923; Blackwelder 1934, 1936	[Clausen 1940]; Peschke et *al.* 1987	462.
Dianous coerulescens	Weinreich 1968	diet undocumented	463.
Eumicrota corruscula (Erichson)	Ashe 1984b	Ashe 1984a, 1984b	464.
Gyrophaena affinis Sahlberg	Ashe 1984b	Ashe 1984a, 1984b	465.
Loeblius nepalensis Pace	Pace 1985	Pace 1985	466.
Megaquedius explanatus	Evans 1942; Cook 1943	Crowson 1981	467.
Pachorhopala jeaneli Levasseur	Levasseur 1965	diet undocumented	468.
Phanerota insigniventris (Cameron)	Ashe 1984b	Ashe 1984a, 1984b	469.
Philonthus decorus (Gravenhorst)	[Blackwelder 1936]; Evans 1965a, 1965c; Weinreich 1968	Balduf 1935; [Clausen 1940]; Crowson 1981; [Peschke et *al.* 1987	470.
Pseudolignota affinis Cameron	Ashe 1984b	Ashe 1984a, 1984b	471.
Staphylinus olens Muller	[Snodgrass 1935, 1960]; [Williams 1938]; Schmitz 1943; Evans 1965c; Weinreich 1968	Balduf 1935; Pesche et *al.* 1987	472.
*Staphylinus** sp.	[Snodgrass 1960]; Bitsch 1966; Crowson 1981	Balduf 1935	473.
Stenus bipunctatus Erichson	[Stickney 1923]; [Blackwelder 1936]; Schmitz 1943; Weinreich 1968	Crowson 1981	474.
*Stenus biguttatus** Linneaus	[Meinert 1887]; Weinreich 1968	Weinreich 1968	475.
Sternotropa brevicornis Cameron	Ashe 1984b	Ashe 1984a, 1984b	476.
*Thinopinus pictus** LeConte	Snodgrass 1935, 1960; Bitsch 1966	[Milne & Milne 1980]	477.

taxon	mouthpart-morphology data	dietary data	no.
Pselaphidae			
Rhinoscepsis bistriatus Linneaus	Park 1942	Park 1942	478.
*Trichonyx sulcicollis** Reichenbach	Besuchet 1956	Besuchet 1956	479.
Sf. **Hydrophiloidea**			
Hydrophilidae			
Acalomicrus pusio Smetana	Smetana 1975	Smetana 1975	480.
Berosus sp.	[Pu 1936]; Cook 1943; Crowson 1967	Smetana 1975	481.
Hydrobius * sp.	Moulins 1959; Bitsch 1966	Crowson 1981; Merritt & Cummins 1984	482.
*Hydrochus squamifer** LeConte	Böving & Craighead 1931	Merritt & Cummins 1984	483.
*Hydrophilus caraboides** Linneaus	[Crampton 1921c]; [Snodgrass 1944, 1960]; Moulins 1959	Milne & Milne 1980	484.
Hydrophilus obtusatus Say	[Smith 1898]; [Berlese 1909]; Stickney 1923; [Golden 1925]; [Pu 1936]; Snodgrass 1947; Richards & Davies 1977	Milne & Milne 1980; Crowson 1981	485.
*Hydrous triangulatis** Say	Anderson 1936; [Anschau 1950]; Peterson 1951	Crowson 1981	486.
*Philhydrus testaceus** Fabricius	Moulins 1959; Bitsch 1966	Crowson 1981	487.
*Sperchus emarginatus** Schall	Böving & Craighead 1931	[White 1983]	488.
Sphaeridium scarabaeoides Linneaus	[Williams 1938]; Dorsey 1943	Pruthi 1969	489.
*Sphaeridium** sp.	Peterson 1951; Bitsch 1966; Quennedey 1965; Crowson 1981	Crowson 1981	490.
Tropisternus glaber Herbst	Williams 1938; Merritt & Cummins 1984	Merritt & Cummins 1984	491.
Georyssidae			
Georyssus laevicollis Germar	Stickney 1923; Williams 1938;	[Merritt & Cummins 1984]	492.
Sphaeritidae			
Sphaerites glabratus (Fabricius)	Stickney 1923; Williams 1938	Crowson 1981	493.
Synteliidae			
Histeridae			
Hister obtusatus Harris	[Stickney 1923]; Williams 1938	[Poulton 1906]; Milne & Milne 1980; Peschke *et al.* 1987	494.
*Hololepta** sp.	Anderson 1936; [Peterson 1951]	[Arnett & Jacques 1981]	495.

taxon	mouthpart-morphology data	dietary data	no.
Sf. Eucinetoidea			
Eucinetidae			
Eucinetus meridionalis Casteinau	[Stickney 1923]; Vit 1977	Crowson 1981; White 1983	496.
*Eucinetus morio** LeConte	Böving & Craighead 1931; Lawrence & Newton 1980	Lawrence & Newton 1980; White 1983	497.
Jentozkus plaumanni Vit	Vit 1977; Chaudonneret 1989a	[Richards & Davies 1977]	498.
Tohklezkus ponticus Vit	Vit 1977, 1981	Crowson 1981; White 1983	499.
Clambidae			
Clambus punctulatum Becker	[Stickney 1923]; Williams 1938; Crowson 1967	[Borror, DeLong & Triplehorn 1976	500.
Scirtidae			
*Elodes marginata** Fabricius	[Carpenter & MacDowell 1912]; Böving & Craighead 1931; Beier 1952; Matsuda 1965	Crowson 1981	501.
*Prionocyphon discoideus** (Say)	Böving & Craighead 1931; Anderson 1936; Merritt & Cummins 1984	McCafferty & Provonsha 1983 1983	502.
Scirtes tibialis Guerin	Lombardi 1928; [Williams 1938]; McCafferty & Provoshna 1983	Merritt & Cummins 1984	503.
Sf. Dascilloidea			
Dascillidae			
*Dascillus cervinus** Linneaus	Gahan 1908; Carpenter & McDowell 1912; Verhoeff 1923; Böving & Craighead 1931	Gahan 1908; Crowson 1981	504.
*Trichentoma childreni** Gray	Gahan 1908	Gahan 1908; [White 1983]	505.
Rhipiceridae			
Sandalus niger Knoch	Stickney 1923; [Williams 1938]	[Clausen 1940]; Crowson 1981	506.
Sf. Scarabaeoidea			
Lucanidae			
Lucanus cervus Linneaus	[Berlese 1909]; Jawlowski 1936; Borror, DeLong and Triplehorn 1976; Richards & Davies 1977	Milne & Milne 1980; Arnett & Jacques 1981; White 1983	507.
*Lucanus cervus** Linneaus	[Böving & Craighead 1931]; Das 1938; Striganova 1967	Milne & Milne 1980; Arnett & Jacques 1981	508.
Pseudolucanus capreolus (Linneaus)	Stickney 1923; Williams 1938	Milne & Milne 1980	509.
*Sinodendron cylindricum** Linneaus	Böving & Craighead 1931; [Das 1938]	[Milne & Milne 1980]; White 1983	510.
Passalidae			
Passalus cornutus Fabricus	Packard 1898; Stickney 1923; Williams 1938	Borror, DeLong & Triplehorn 1976	511.

taxon	mouthpart-morphology data	dietary data	no.
*Passalus cornutus** Fabricius	[Crampton 1928b]; Hayes 1928; Böving & Craighead 1931	Crowson 1981	512.
*Popilius disjunctus** Illiger	Hayes 1928; Hiznay & Krause 1955	Borror, DeLong & Triplehorn 1976	513.
Trogidae			
*Trox scaber** Linneaus	Böving & Craighead 1931	Bertin 1923; White 1983; Peschke *et al.* 1987	514.
Ceratocanthidae			
Pleocomidae			
Geotrupidae			
Geotrupes stercorarius Linneaus	Bertin 1923; [Williams 1938]; [Howden 1955]	Howden 1955; Peschke *et al.* 1987	515.
*Geotrupes splendidus** Fabricius	[Carpenter & McDowell 1912]; [Hayes 1928]; Howden 1955	White 1983; [Peschke *et al.*	516.
Diphyllostomatidae			
Diphyllostoma linsleyi Fall	Holloway 1972	Holloway 1972	517.
Scarabaeidae			
Amphimallon majalis (Razoymowski)	Butt 1944	Butt 1944; Johnson & Lyon 1976	518.
*Amphimallon majalis** (Razoymowski)	Butt 1944	Johnson & Lyon 1976	519.
*Anastrategus splendens** Beauvois	Böving & Craighead 1931	[White 1983]	520.
*Aserica castanea** Arrow	Böving & Craighead 1931	[White 1983]	521.
Cetonia aurata Linneaus	Bertin 1923; Barth 1985	Bertin 1923; Crowson 1981	522.
*Melolontha hippocastani** Fabricius	Subklew 1938	Subklew 1938; [Lawrence 1982]	523.
Melolontha vulgaris Fabricius	Kadic 1902; Bertin 1923; Osterwald 1954	Bertin 1923; Crowson 1981	524.
Neodon pecuarius (Reiche)	Carne 1957	Carne 1957	525.
Oryctes grypus	Bertin 1923	Bertin 1923; Hill 1983	526.
*Oryctes nasicornis** Linneaus	Crome 1957; Bitsch 1966	[Carne 1957]	527.
*Phyllophaga rugosa** Melsheimer	Peterson 1951	Bertin 1923; Brues 1972; Lawton 1976	528.
Pimelopsis porcellus Erichson	Carne 1957	Carne 1957	529.
Popillia japonica Newman	Hayes 1928; Dorsey 1943	Westcott 1964; Johnson & Lyon 1976	530.

taxon	mouthpart morphology data	dietary data	no.
*Popillia japonica** Newman	Snodgrass 1928, 1935, 1947, 1950, 1960; Böving & Craighead 1931; Peterson 1951; Bitsch 1966	Johnson & Lyon 1976; Milne & Milne 1980	531.
Scarabaeus sacer Linneaus	Bertin 1923	Bertin 1923; Carne 1957	532.
Sf. **Byrrhoidea**			
Byrrhidae			
Byrrhus americana LeConte	Stickney 1923; Williams 1938	Crowson 1981	533.
*Byrrhus fasciatus** Forster	Böving & Craighead 1931; [Anderson 1936]; [Dorsey 1943]; [Peterson 1951]	Crowson 1981	534.
Sf. **Buprestoidea**			
Buprestidae			
*Chalcophora virginiensis** Drury	Crampton 1921c; Böving & Craighead 1931; [Snodgrass 1947, 1960]; Peterson 1951	Uvarov 1928; [Milne & Milne 1980]	535.
*Chrysobothris femorata** Olivier	Böving & Craignead 1931; Peterson 1951	Boving & Craighead 1931; Peterson 1951	536.
Sf. **Dryopoidea**			
Eulichadidae			
Callirhiphidae			
Ptilodactylidae			
*Ptilodactyla serricollis** (Say)	Böving & Craighead 1931; Anderson 1936; Dorsey 1943	Crowson 1981	537.
Chelonariidae			
Chelonarium ornatum Klug	[Stickney 1923]; Williams 1938	White 1983	538.
Heteroceridae			
Heterocerus parallelus Krynick	[Stickney 1923]; Williams 1938; [White 1983]	Crowson 1981	539.
Limnichidae			
*Limnius troglodytes** Gyllenhal	Böving & Craignead 1931; [Delachambre 1965]; [Bitsch 1966]	[Merritt & Cummins 1984]	540.
Lutrochidae			
Lutrochus arizonicus Brown & Murvosh	Brown & Murvosh 1970	Merritt & Cummings 1984	541.
Dryopidae			
Helichus fastigatus (Say)	[Stickney 1923]; Dorsey 1943; McCafferty & Provoshna 1983	McCafferty & Provoshna 1983; Merritt & Cummins 1984	542.
*Helichus** sp.	Böving & Craighead 1931; [Peterson 1951]	Peterson 1951	543.
*Riolus** sp.	Marvillet 1960	McCafferty & Provoshna 1983	544.
Elminthidae			
*Stenelmis crenata** Say	Böving & Craighead 1931; [Peterson 1951]	Merritt & Cummins 1984	545.
Psephenidae			
Psephenus lecontei (LeConte)	Stickney 1923; Williams 1938	Arnett 1963; Crowson 1981; Merritt & Cummins 1984	546.

taxon	mouthpart-morphology data	dietary data	no.
Sf. Elateroidea			
Artematopidae			
_Artematopus discoidalis_* Pic	Costa, Cassari-Chen & Vanin 1985	Costa, Cassari-Chen & Vanin 1985	547.
Cerophytidae			
Elateridae			
_Agriotes_* sp.	[Rymer-Roberts 1931]; Das 1938; Peterson 1951	Rymer-Roberts 1921; Clausen 1940; Crowson 1981	548.
Alaus oculatus Linneaus	Stickney 1923; Williams 1938	Milne & Milne 1980; Arnett & Jacques 1981	549.
_Alaus oculatus_* Linneaus	Snodgrass 1947; Peterson 1951	Peterson 1951	550.
_Horistonotus uhlerii_* Horn	Hyslop 1915; Böving & Craighead 1931	Hyslop 1915	551.
Neotrichophorus carolinensis (Schaeffer)	Dorsey 1943	Crowson 1981	552.
_Parallelostethus attenuatus_* (Say)	Dorsey 1943; Peterson 1951; Bitsch 1966	Crowson 1981	553.
Cebrionidae			
Cebrio bicolor	Stickney 1923; Williams 1938; White 1983	White 1983	554.
_Cebrio attenuatus_* Schaeffer	Böving & Craighead 1931	White 1983	555.
_Oestodes tenuicollis_* Randall	Böving & Craighead 1931	[White 1983]	556.
Throscidae			
Throscus dermestoides Linneaus	[Stickney 1923]; Williams 1938	Borror, DeLong & Triplehorn 1976	557.
Perothopidae			
Eucnemidae			
Eucnemis capucina Ahrens	Williams 1938; Crowson 1981	Crowson 1981	558.
_Melasis rufipennis_* Horn	Böving & Craighead 1931; [Peterson 1951]; Crowson 1981	Peterson 1951; [Crowson 1981]	559.
Rhinorhipidae			
Rhinorhipus tamboriensis Lawrence	Lawrence 1987	Lawrence 1987	560.
Sf. Cantharoidea			
Brachypsectridae			
_Brachyspectra fulva_* LeConte	Böving & Craighead 1931	White 1983	561.
Cneoglossidae			
Homalisidae			
Lycidae			
_Calochromis tarsalis_*	Gardner 1946; Crowson 1981	Gardner 1946; Crowson 1981	562.
_Calopteron reticulatum_* Fabricius	Böving & Craighead 1931; [Peterson 1951]	[Peterson 1951]; Crowson 1981	563.

taxon	mouthpart-morphology data	dietary data	no.
*Eros aurora** Herbst	Verhoeff 1923; [Bőving & Craighead 1931]	[White 1983]; Crowson 1981	564.
Lycus sp.	Crampton 1923; [Arnett 1963]	Crowson 1981; [Arnett & Jacques 1981]	565.
Drilidae			
*Drilius concolor** Ahrens	Bőving & Craighead 1931	Bőving & Craighead 1931	566.
Phenogodidae			
*Phenogodes laticollis** LeConte	Bőving & Craighead 1931; Peterson 1951	Peterson 1951; White 1983	567.
Phenogodes sp.	[Stickney 1923]; Williams 1938; [Arnett 1963]	Clausen 1940; Crowson 1981	568.
Telegeusidae			
Lampyridae			
*Lampyris noctiluca** Linneaus	Vogel 1915; Bőving & Craighead 1931; Jeannel 1960	Clausen 1940; Peterson 1951	569.
*Lamprophorus tenebrosus** Walker	Raj 1943; Gardner 1946	Gardner 1946; Arnett 1963	570.
*Luciola dubia** Olivier	Gardner 1946; [Arnett 1963]	[Clausen 1940]	571.
*Photinus pyralis** Linneaus	Bőving & Craighead 1931; [Peterson 1951]	Peterson 1951; White 1983	572.
*Photurus pennsylvanica** DeGeer	Bőving & Craighead 1931; [Peterson 1951]	Peterson 1951; White 1983	573.
Omethidae			
Cantharidae			
Cantharis andersoni Forster	[Stickney 1923]; Williams 1938	Crowson 1981	574.
*Cantharis rustica** Fall	Bőving & Craighead 1931; [Peterson 1951]; [Bitsch 1966]	Crowson 1981	575.
Chauliognathus pennsylvanicus (DeGeer)	[Crampton 1921c]; Stickney 1923; Campau 1940; Dorsey 1943; [Arnett 1963]	Clausen 1940; Milne & Milne 1980; Arnett & Jacques 1981	576.
Sf. Dermestoidea			
Derodontidae			
Derodontus maculatus Melsheimer	Stickney 1923; Williams 1938; [Lawrence & Hlavac 1979]; Crowson 1981	Crowson 1981	577.
Nosodendridae			
Nosodendron californicum Horn	[Stickney 1923]; Dorsey 1943	Crowson 1981	578.
*Nosodendron unicolor** Say	Bőving & Craighead 1931; [Anderson 1936]; Peterson 1951	Crowson 1981	579.
Dermestidae			
*Anthrenus fasciatus** Herbst	[Bőving & Craighead 1931]; Pradhan 1950	Uvarov 1928; Crowson 1981	580.

taxon	mouthpart-morphology data	dietary data	no.
Dermestes lardarius Linneaus	Stickney 1923; [Robinson 1930]; Williams 1938; [Dorsey 1943]; [Homonichl 1976]	Crowson 1981; Peschke *et al.* 1987	581.
*Dermestes vulpinus** Fabricius	Robinson 1930; [Boving & Craighead 1931]; Das 1938; [DuPorte 1946]; [Peterson 1950]	[Balduf 1935]; [Peschke et al. 1987	582.
Jacobsoniidae			
*Saphophagus minutus** Sharp	Sharp 1886, Crowson 1959	diet undocumented	583.
Sf. Bostrichoidea			
Bostrichidae			
Apatides fortis LeConte	Dorsey 1943; Arnett 1963	[Richards & Davies 1977]	584.
*Apatides fortis** LeConte	Dorsey 1943; Bitsch 1966	Crowson 1981	585.
Lyctus linearis (Goeze)	[Stickney 1923]; Williams 1938	White 1983	586.
*Scobicia declivis** LeConte	Böving & Craighead 1931	[Arnett 1963]; White 1983	587.
Anobiidae			
*Anobium striatum**	Verhoeff 1923	White 1983	588.
*Trichodesma klagesi** Fallen	Böving & Craighead 1931; [Snodgrass 1947]; [Peterson 1951]	Crowson 1981	589.
Ptinidae			
Oligomerus brunneus Olivier	Stickney 1923; Williams 1938	Crowson 1981	590.
*Oligomerus fur** Linneaus	Böving & Craighead 1931; [Das 1938]; [Peterson 1951]	[Crowson 1981]; White 1983	591.
Sf. Lymexyloidea			
Lymexylidae			
Hylecoetus lugubris Say	Stickney 1923; [Williams 1938]; Dorsey 1943	Crowson 1981	592.
Sf. Cleroidea			
Phloiophilidae			
Trogossitidae			
*Calitys scabra** Thunberg	Böving & Craighead 1931	[White 1983]	593.
*Promanus** sp.	[Arnett 1963]; Crowson 1981	[Crowson 1981]	594.
*Tenebroides nanus** Melsheimer	Böving & Craighead 1931; [Das 1938]; [Peterson 1951]; Hinton 1963	[Johnson & Lyon 1976]	595.
*Temnochila viriscens** Fabricius	Böving & Craighead 1931	[White 1983]	596.
Chaetosomatidae			
Cleridae			
*Callimeris arcufer** Chapin	Böving & Craighead 1931	[White 1983]	597.
*Enoclarus lecontei** Wolcott	Böving & Craighead 1931; [Peterson 1951]	Peterson 1951	598.

taxon	mouthpart-morphology data	dietary data	no.
*Necrobia rufipes** (Fabricius)	Peterson 1951	Peterson 1951; [Peschke et *al.* 1987]	599.
Trichodes ornatus Say	[Stickney 1923]; Williams 1938	Clausen 1940; [Milne & Milne 1981]	600.
Phycosecidae			
Acanthocnemidae			
Melyridae			
*Dasytes coeruleus** DeGeer	Böving & Craighead 1931	[White 1931]	601.
Malachius bipustulatus Linneaus	[Williams 1938]; Schicha 1967; Barth 1985	Schicha 1967; [Arnett & Jacques 1981]	602.
Sf. Cucjoidea			
Protocucujidae			
Sphindidae			
Sphindus dubius Gyllenhal	Stickney 1923; Williams 1938	Crowson 1981	603.
Nitidulidae			
*Glischrochilus obtusatus** Say	Verhoeff 1923; Böving & Craighead 1931	Swan & Papp 1972; [White 1983]; [Peschke et *al.* 1987]	604.
*Prometopia sexmaculata** (Say)	Böving & Craighead 1931	Swan & Papp 1972; White 1983	605.
Rhizophagidae			
Rhizophagus picipes Walker	[Stickney 1923]; [Verhoeff 1923]; Williams 1938	Clausen 1940	606.
Boganiidae			
Boganium armstrongi Sen Gupta & Crowson	Sen Gupta & Crowson 1966	Sen Gupta & Crowson 1966	607.
Phloeostichidae			
*Rhophalobrachium clavipes** Bohemann	Sen Gupta & Crowson 1969b; [Crowson 1973]	Sen Gupta & Crowson; Lawrence 1982	608.
Helotidae			
*Helota gemmata** Gorham	Fukuda 1943; Rymer-Roberts 1958; Lawrence 1982	[Lawrence 1982]	609.
Cucujidae			
Cucujus clavipes Fabricius	Stickney 1923; Williams 1938	Milne & Milne 1980	610.
*Cucujus clavipes** Fabricius	Böving & Craighead 1931; Anderson 1936; Peterson 1951	Milne & Milne 1980	611.
*Oryzaephilus surinamensis** (Linneaus)	Böving & Craighead 1931; Anderson 1936; Peterson 1951; Honomichl 1978	Crowson 1981; Hill 1983	612.
*Telephanus ?pallidus** Schauf.	Böving & Craighead 1931	White 1983	613.
Cavognathidae			
Cavognatha pullivora Crowson	Crowson 1964; Sen Gupta & Crowson 1969b	Sen Gupta & Crowson 1969b	614.

taxon	mouthpart-morphology data	dietary data	no.
Cryptophagidae			
*Antherophagus ochraceus** Melsheimer	Verhoeff 1923; Böving & Craighead 1931; Arnett 1963	Crowson 1981	615.
*Cryptophagus saginatus** Sturmer	Böving & Craighead 1931; Peterson 1951]	Peterson 1951	616.
Propalticidae			
*Propalticus simplex** Crowson & Sen Gupta	Crowson & Sen Gupta 1969b	diet undocumented	617.
Lamingtoniidae			
Lamingtonium binnaburrense Sen Gupta & Crowson	Sen Gupta & Crowson 1969a	Sen Gupta & Crowson 1969a	618.
Hobartiidae			
Hydnobioides pubescens Sen Gupta & Crowson	Sen Gupta & Crowson 1966, 1969b	Sen Gupta & Crowson 1966	619.
Languriidae			
*Languria angustata** Beauvois	Böving & Craighead 1931; [Peterson 1951]; [Baker & Ellsbury 1988]	Peterson 1951	620.
Erotylidae			
Megalodacne fasciata Fabricius	Stickney 1923; [Williams 1938]; Rymer-Roberts 1958	Chujo 1969	621.
*Tritoma unicolor** Say	Böving & Craighead 1931; Anderson 1936; [Peterson 1951]; [Rymer-Roberts 1958]	Chujo 1969	622.
Phalacridae			
Phalacrus grossus Erichson	Stickney 1923; Williams 1938	D'Aguilar 1944; Crowson 1981	623.
Cerylonidae			
Aculagnathus mirabilis Oke	Besuchet 1972; Sen Gupta & Crowson 1973	Crowson 1981; [White 1983]	624.
Axiocerylon cavicolle Grouvelle	Sen Gupta & Crowson 1973	Sen Gupta & Crowson 1973	625.
Cautomus sugerens Besuchet	Besuchet 1972; Dajoz 1976	[Lawrence & Stephan 1975]; [Crowson 1981]	626.
Cerylcautomus floridensis Sen Gupta & Crowson	Sen Gupta & Crowson 1973	[Lawrence & Stephan 1975]; [White 1983]	627.
Cerylon fagi Brisout	[Sen Gupta & Crowson 1973]; [Lawrence & Stephan 1975]; Dajoz 1976	[Lawrence & Stephan 1975]; Dajoz 1976	628.
Lapecautomus dybasi Sen Gupta & Crowson	Sen Gupta & Crowson 1973	[Crowson 1981]; [White 1983]	629.
Neoglyptoides jamaciensis Dajoz	Dajoz 1976	Dajoz 1976	630.

taxon	mouthpart-morphology data	dietary data	no.
*Philothermus bicavus** Sharp	Sen Gupta & Crowson 1973; [Dajoz 1976]; Crowson 1981	Dajoz 1976	631.
Corylophidae			
*Arthrolips?** sp.	Bōving & Craighead 1931; Peterson 1951	Peterson 1951	632.
Hoplicnema sallaei Matthews	Pakaluk 1987	Pakaluk 1987	633.
Discolomidae			
*Discoloma cassideum** Reutter	Emden 1932	Emden 1932	634.
Coccinellidae			
Anatis quindecimpunctata (Olivier)	Kellogg 1902; [Evans 1921]; Williams 1938; Arnett 1963	Hodek 1973	635.
*Chilocorus bivulnerus** Mulsant	Gage 1920	White 1983	636.
Coccinella septempunctata (Linneaus)	Pradhan 1939a, 1939b; Grinfel'd 1975; Richards & Davies 1977	[Milne & Milne 1980]; Crowson 1981	637.
Epilachna varivestris Mulsant	[Pradhan 1939a, 1939b]; Butt 1951	Clausen 1940; Crowson 1981; Hill 1983	638.
*Microweisea misella** LeConte	Gage 1920	White 1983	639.
Sphaerosomatidae			
Endomychidae			
*Endomychus coccineus** Linneaus	Bōving & Craighead 1931; [Peterson 1951]	Peterson 1951	640.
*Lycoperdina succinata** Linneaus	Boving & Craighead 1931; Peterson 1951]	Peterson 1951; [White 1983]	641.
*Mycetaea hirta** Marsham	Verhoeff 1923; Bōving & Craighead 1931	Richards & Davies 1977; [White 1983]	642.
Lathridiidae			
*Cartodere costulata** Reitter	Bōving & Craighead 1931; [Peterson 1951]	Peterson 1951	643.
*Hesperobaenus** sp.	Bōving & Craighead 1931	[White 1983]	644.
Biphyllidae			
Byturidae			
*Byturus tomentosus** Fabricius	Verhoeff 1923; Bōving & Craighead 1931; Peterson 1951	Peterson 1951	645.
Sf. Tenebrionoidea			
Mycetophagidae			
Mycetophagus punctatus Say	Stickney 1923; Williams 1938	Crowson 1981	646.
*Mycetophagus punctatus** Say	Bōving & Craighead 1931; [Anderson 1936]; Peterson 1951	Crowson 1981	647.
Tetratomidae			
Penthe obliquata (Fabricius)	Stickney 1923; Williams 1938; Arnett 1963	[Swan & Papp 1972]; White 1983	648.

taxon	mouthpart-morphology data	dietary data	no.
Ciidae			
*Cis boleti** Scopoli	Verhfoeff 1923; [Böving & Craighead 1931]	Crowson 1981	649.
Melandryidae			
*Melandrya striata** Say	Böving & Craighead 1931; [Snodgrass 1935, 1960]; Peterson 1951	Peterson 1951; [White 1983]	650.
Mordellidae			
Mordella quadripunctata (Say)	Dorsey 1943; Arnett 1963	[Arnett & Jacques 1981] Crowson 1981	651.
Tomoxia bidentata (Say)	Stickney 1923; Williams 1938	[Crowson 1981]	652.
Rhipiphoridae			
Macrosiagon ferrungineum Fabricius	[Rivnay 1929]; Grandi 1936, 1937, 1959	Clausen 1940; [White 1983]	653.
*Macrosiagon ferrugineum** Fabricius	Grandi 1936, 1937, 1959	Crowson 1981	654.
Rhipiphorous dimidiatus Fabricius	Crampton 1923a, 1923b; Stickney 1923; [Rivnay 1929]; Williams 1938	Clausen 1940	655.
*Rhizostylops inquirendus** Silvestri	Silvestri 1905	[White 1983]	656.
Archaeocrypticidae			
Pterogeniidae			
*Pterogenius nietneri** Candeze	Lawrence 1977	Lawrence 1977	657.
Colydiidae			
*Aulonium tuberculatum** LeConte	Böving & Craighead 1931	Clausen 1940; [White 1983]	658.
*Synchita fuliginosa** Melsheimer	Böving & Craighead 1931	Peterson 1951; [White 1983]	659.
Monommidae			
*Hyporhagus texanus** Linell	Peterson 1951; Arnett 1963	Peterson 1951; [White 1983]	660.
Zopheridae			
*Phellopsis obcordata** Kirby	Böving & Craighead 1931; Peterson 1951]	[Peterson 1951]	661.
Perimylopidae			
*Perimylops antarcticus** Müller	St. George 1939; Watt 1970	[Watt 1970]	662.
Chalcodryidae			
*Chalcodrya** sp.	Watt 1974	Watt 1974	663.
Tenebrionidae			
Alobates pennsylvanica (DeGeer)	Stickney 1923; Williams 1938	White 1983	664.
*Alobates pennsylvanica** (DeGeer)	Böving & Craighead 1931	White 1983	665.
Arthromacra aenea (Say)	Stickney 1923; Williams 1938	White 1983	666.
*Hoplocephala ferruginea** LeConte	Böving & Craighead 1931	White 1983	667.
*Hymenorus pilosus** Melsheimer	Böving & Craighead 1931; [Anderson 1936]	White 1983	668.

taxon	mouthpart-morphology data	dietary data	no.
*Merinus laevis** Olivier	Anderson 1936; Crowson 1981	[White 1983]	669.
Pimelia cephalotes Beauvois	Medvedev 1960	Crowson 1981	670.
*Scotobates calcaratus** Fabricius	Dorsey 1943; Bitsch 1966	[White 1983]	671.
Tenebrio molitor Linneaus	[Crampton 1921c]; Stickney 1923; Doyen 1966; Trombetta 1976	Milne & Milne 1980	672.
*Tenebrio** sp.	Das 1938; DuPorte 1946; [Peterson 1951]	Milne & Milne 1980	673.
Cephaloidae			
Cephaloon lepturides Newman	Stickney 1923; Williams 1938	White 1983	674.
Meloidae			
Epicauta pennsylvanica (DeGeer)	[Stickney 1923]; Snodgrass 1928, [1932, 1960]; Weinreich 1968	Clausen 1940; Milne & Milne 1980; Hill 1983	675.
*Epicauta pennsylvanica** (DeGeer)	Böving & Craighead 1931; [Peterson 1951]	Milne & Milne 1980; Hill 1983	676.
Leptopalpus rostratus Fabricius	Handschin 1929; Jeanell 1960; Grinfel'd 1975	Clausen 1940; Crowson 1981	677.
Macrobasis immaculata (Say)	Dorsey 1943; Arnett 1963	Clausen 1940	678.
Nemognatha piezata Fabricius	Hagen 1881; Smith 1898; Packard 1898; Berlese 1909; Crampton 1923b; Williams 1938; Grinfel'd 1975; Barth 1985	Clausen 1940; [Arnett & Jacques 1981]	679.
*Zonitis bilineata** Say	Böving & Craighead 1931	[White 1983]	680.
Oedomeridae			
*Calopus angustus** LeConte	Böving & Craighead 1931	White 1983	681.
*Nacerdes melanura** (Linneaus)	Peterson 1951; Rozen 1958	Peterson 1951; Rozen 1958	682.
Prostomidae			
*Prostomis mandibularis** Fabricius	Böving & Craighead 1931	[White 1983]	683.
Synchroidae			
*Synchroa punctata** Newman	Böving & Craighead 1931; Anderson 1936; Peterson 1951	Peterson 1951	684.
Mycteridae			
*Mycterus curculionides** Fabricius	Crowson & de Viedma 1964	Crowson & de Viedma 1964	685.
Boridae			
Trichentomidae			
*Trichentoma childreni** Gray	Gahan 1908	Gahan 1908; [White 1983]	686.
Pythidae			
Pytho americanus Kirby	[Stickney 1923]; Williams 1938	diet undocumented	687.
*Pytho niger** Kirby	Böving & Craighead 1931; [Anderson 1936]	White 1983	688.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
Pyrochroidae			
*Neopyrochroa femoralis** LeConte	Böving & Craighead 1931; Peterson 1951	White 1983	689.
Salpingidae			
*Othnius umbrosus** LeConte	Böving & Craighead 1931	Balduf 1935; [Arnett 1963]	690.
*Aegialites debilis** Mannerheim	Böving & Craighead 1931	[Arnett 1963]	691.
Anthicidae			
*Anthicus** sp.	Böving & Craighead 1931; Anderson 1936	Clausen 1940	692.
Notoxus calcaratus Horn	[Stickney 1923]; Williams 1938	Clausen 1940	693.
Scraptiidae			
*Scraptia sericea** Melsheimer	Böving & Craighead 1931	[White 1983]	694.
Euglenidae			
Sf. Chrysomeloidea			
Cerambycidae			
Cyllene robiniae Forster	Goldman 1933; Dorsey 1943	Goldman 1933; [White 1983]	695.
Desmocerus palliatus Forster	Goldman 1933; [White 1983]	Milne & Milne 1980; Arnett & Jacques 1981	696.
Leptura sp.	Gahan 1906; Goldman 1933; White 1983	Uvarov 1928; Goldman 1933; Milne & Milne 1980	697.
Monochamus titillator Fabricius	Goldman 1933; DuPorte 1946, 1962c; Arnett 1963; White 1983	Goldman 1933; Milne & Milne 1980; Arnett & Jacques 1981	698.
Oberea tripunctata Olivier	Goldman 1933; Johnson & Lyon 1976	Goldman 1933; Johnson & Lyon 1976	699.
*Orthosoma** sp.	Böving & Craighead 1931; Anderson 1936; Peterson 1951	Goldman 1933; [Crowson 1981]	700.
*Rhagium** sp.	Packard 1898; Böving & Craighead 1931; Das 1938	Uvarov 1928; Milne & Milne 1980	701.
Tetraopes tetraophthalmus (Forster)	Stickney 1923; Goldman 1933; Williams 1938	Goldman 1933; Milne & Milne 1980; [Arnett & Jacques 1981]	702.
Bruchidae			
Bruchus discoideus Say	Williams 1938; [White 1983]	Crowson 1981; [White 1983]	703.
*Bruchus pisorum** Linneaus	Böving 1927b; Böving & Craighead 1931; Peterson 1951	Swan & Papp 1972	704.
Chrysomelidae			
Atalasis sagroides Lacordaire	Munros 1959	[White 1983]	705.
*Crioceris asparagi** Linneaus	Böving & Craighead 1931; Peterson 1951	Peterson 1951	706.

taxon	mouthpart-morphology data	dietary data	no.
Galerucella birmanica (Jacoby)	Khatib 1946	Crowson 1981	707.
*Galerucella xanthomelaena** Schaeffer	Böving & Craighead 1931; [Anderson 1936]; [Peterson 1951]	Crowson 1981	708.
*Hispa testacea** Linneaus	Grandi 1959	Needham, Frost & Tothill 1928	709.
Leptinotarsa decemlineata (Say)	Stickney 1923; Williams 1938; Dorsey 1943	[Clausen 1940]; Milne & Milne Milne 1980; Crowson 1981	710.
Megamerus kingi MacLeay	Monros 1959	[White 1983]	711.
*Phyllotreta nemorum** Linneaus	Grandi 1959; Needham, Frost & 1928	Needham, Frost & Tothill 1928; Hill 1983	712.
*Sphaeroderma testaceum** Fabricius	Böving & Craighead 1931; [Grandi 1959]	diet undocumented	713.
*Zeugophora subspinosa** Fabricius	Needham, Frost & Tothill 1928; [Böving & Craighead 1931]; Grandi 1959; [Striganova 1967]	Needham, Frost & Tothill 1928	714.
Sf. Curculionoidea			
Nemonychidae			
Cimberis attelaboides Fabricius	[Stickney 1923]; [Ting 1936]; Crowson 1967	Crowson 1981	715.
Anthribidae			
Araecerus fasciatus DeGeer	Ting 1936; Morimoto 1962	[Richards & Davies 1977]; [White 1983]	716.
*Araecerus fasciatus** DeGeer	Böving & Craighead 1931; Peterson 1951	Peterson 1951	717.
Euparius marmoreus (Olivier)	Dorsey 1943; [Morimoto 1962]; Arnett 1963	[Swan & Papp 1972]; [White 1983]	718.
*Euparius marmoreus** (Olivier)	Böving & Craighead 1931	[White 1983]	719.
Oxycorynidae			
Rhopalotria glossoni Schaeffer	Ting 1936; Muñiz & Barrera 1969]	Muñiz & Barrera 1969; Crowson 1981	720.
Belidae			
Dicordylus binotatus (Phillipi)	Vanin 1976	Vanin 1976	721.
Aglycyderidae			
*Proterhinus anthracias** Perkins	Böving & Craighead 1931; Anderson 1941	Anderson 1941	722.
Attelabidae			
*Rhynchites aenus** Boheman	Böving & Craighead 1931	[White 1983]	723.

taxon	mouthpart-morphology data	dietary data	no.
Rhynchites auratus Scopoli	[Stickney 1923]; [Ting 1933, 1936]; [Morimoto 1962]; Brack-Egg 1973	[Johnson & Lyon 1976]; Milne & Milne 1980]	724.
Brentidae			
Eupsalis minuta Drury	Stickney 1923; Ting 1936; Williams 1938	[Milne & Milne 1980]	725.
*Eupsalis minuta** Drury	Bőving & Craighead 1931	[White 1983]	726.
Apionidae			
Apion stronglydontis Wagner	Ting 1936; [Morimoto 1962]	[Swan & Papp 1972]	727.
Ithyceridae			
Ithycerus novaeboracensis (Forster)	Stickney 1923; Ting 1936; Williams 1938	White 1983	728.
Curculionidae			
Calandra granaria Linneaus	Dennell 1942; [Pajni & Chhibba 1972]	[Richards & Davies 1977]; [White 1983]	729.
*Calandra granaria** Linneaus	Das 1938; Peterson 1951	Crowson 1981	730.
Caulophilus latinasus Say	Crowson 1967	[Davidson & Lyon 1986]	731.
*Cionus oleus** Fabricius	[Bőving & Craighead 1931]; [Grandi 1959]	Crowson 1981	732.
Cionus scrophulariae Linneaus	Dönges 1954	Uvarov 1928	733.
Curculio caryae (Horn)	[McClenahan 1904]; Ting [1933], 1936; [Morimoto 1962]; Borror, DeLong & Triplehorn 1976	Swan & Papp 1972; Davidson & Lyon 1986	734.
Dendroctonus valens LeConte	Stickney 1923; Chamberlin 1939; Williams 1938	Johnson & Lyon 1976	735.
*Eumycteris saccharidis** Barber	Bőving 1927a	Bőving 1927a	736.
Ips concinnus (Mannerheim)	Ting 1936; Chamberlin 1939; [Morimoto 1962]; Striganova 1967	[Johnson & Lyon 1976]; Milne & Milne 1980	737.
Lixus concavus Say	[Stickney 1923]; Ting 1936; Williams 1938; [Morimoto 1962]	Swan & Papp 1972	738.
Mononychus vulpeculus Fabricius	McClenahan 1904	McClenahan 1904	739.
Pantomorus leucoloma Boheman	[Ting 1936]; Dorsey 1943	[Johnson & Lyon 1976]	740.
Pissodes strobi (Peck)	Richards & Davies 1977	Johnson & Lyon 1976	741.
Platypus australis Chapuis	[Stickney 1923]; Ting 1936; [Williams 1938]; [Morimoto 1962]	Richards & Davies 1977; White 1983	742.

taxon	mouthpart-morphology data	dietary data	no.
*Rhynchaenus alni** Fabricius	Grandi 1959; [Peterson 1951]	[Johnson & Lyon 1976]	743.
Scolytus piceae Swaine	Swaine 1910; [Stickney 1923];	Swaine 1910; [Johnson & Lyon 1976]	744.
STREPSIPTERA			
So. Mengenillidia			
Sf. Mengenilloidea			
Mengenillidae			
Mengenilla theryi (Hofeneder)	[Pierce 1918]; [Bohart 1946b];	Bohart 1946b; Arnett 1963	745.
Eoxenos laboulbenei Peyerimhoff	Parker & Smith 1933; Bohart 1946b	Parker & Smith 1933; Bohart 1946b	746.
*Eoxenos laboulbenei** Peyerimhoff [m.]	Parker & Smith 1933; Bohart 1946b	Parker & Smith 1933; Bohart 1946b	747.
*Eoxenos laboulbenei** Peyerimhoff [f.]	Parker & Smith 1933; Bohart 1946b	Parker & Smith 1933; Bohart 1946b	748.
So. Stylopidia			
Sf. Mengeoidea			
Corioxenidae			
*Callipharixenos muiri** Pierce	Pierce 1918; Bohart 1946b	Bohart 1946b; Arnett 1963	749.
Sf. Bohartilloidea			
Bohartillidae			
Sf. Halictophagoidea			
Halictophagidae			
Halictophagus philaroniae Bohart	Bohart [1943], 1946a; [Kinzelbach 1966]	Bohart 1946b; Arnett 1963	750.
*Halictophagus zanzibarae** Bohart	Bohart [1943], 1962	Bohart 1946b, 1962	751.
Sf. Stylopoidea			
Elenchidae			
Elenchus koebeli (Pierce)	Bohart 1946b; [Kinzelbach 1966]	Bohart 1946b; Arnett 1963	752.
*Elenchus koebeli** (Pierce)	Bohart 1946b	Bohart 1946b; Arnett 1963	753.
Myrmecolacidae			
Caenocholax hoberlandti Linneaus	[Pierce 1918]; [Bohart 1946b]; [Kinzelbach 1966]	Bohart 1946b; Arnett 1963	754.
Stylopidae			
Stylops pacifica Bohart	Bohart 1946b; [Kinzelbach 1966]	Bohart 1946b; Arnett 1963	755.
Xenos vesparum Rossi	[Pierce 1918]; [Crampton 1923b]; [Bohart 1946b]; Kinzelbach 1966; Crowson 1981	Bohart 1946b; Arnett 1963	756.

taxon	mouthpart-morphology data	dietary data	no.
MECOPTERA			
So. Protomecoptera			
Meropeidae			
Merope tuber Newman	Crampton 1917b, 1932; Otanes 1922; Hepburn 1969	[Byers 1973]	757.
Notiothaumidae			
Notiothauma reedi (MacLachlan)	Hepburn 1969	diet undocumented	758.
So. Eumecoptera			
Choristidae			
Chorista australis Klug	Tillyard 1935; Hepburn 1969	[Clausen 1940]; [Pruthi 1969]	759.
Nannochoristidae			
Nannochorista dipteroides Tillyard	Crampton 1921a, 1923b, 1925, 1942; Tillyard 1935; Hoyt 1952; Hepburn 1969	Richards & Davies 1977	760.
Panorpidae			
Apteropanorpa tasmanica Tillyard	Hepburn 1969	[Clausen 1940]; Pruthi 1969	761.
Brachypanorpa carolinensis (Banks)	[Ferris 1942]; Hepburn 1969	[Byers 1965]; Arnett 1985	762.
_Panorpa communis_* Linneaus	[Crampton 1917b, 1921c] Das 1938; Bierbrodt 1943; Snodgrass 1947	Clausen 1940; Peterson 1951	763.
Panorpa nuptialis Gerstaecker	[Packard 1889]; [Smith 1898]; [Crampton 1921c, 1923a, 1923b]; [Otanes 1922]; Hetrick 1935; [Heddergott 1938]; Ferris & Rees 1939	[Miyake 1912]; [Arnett & Jacques 1981	764.
Panorpodes paradoxa MacLachlan	Crampton 1917b, 1923b; [Otanes 1922]; Issiki 1933	[Byers 1965]; Arnett 1985	765.
Bittacidae			
Bittacus pilicornis Westwood	[Smith 1889]; [Crampton 1917b, 1923b]; [Otanes 1922]; Setty 1940; [Hepburn 1969]	Setty 1940; [Borror & White 1970]	766.
_Bittacus pilicornis_* Westwood	Setty 1940, [1941]; Peterson 1951	Setty 1940; Clausen 1940	767.
Neobittacus blancheti	[Tillyard 1935]; Hepburn 1969	[Borror & White 1970]	768.
Apterobittacidae			
Apterobittacus apterus (MacLachlan)	Otanes 1922; Hepburn 1969	Carpenter 1931; Arnett 1985	769.
_Apterobittacus apterus_* (MacLachlan)	Applegarth 1939; Cook 1944; Snodgrass 1947	[Milne & Milne 1980]; Byers 1983	770.
So. Neomecoptera			
Boreidae			
_Boreus brumalis_* Fitch	Peterson 1951	Peterson 1951	771.
Boreus nivoriundus Fitch	[Packard 1889]; Otanes 1922; [Crampton 1942]; [Hepburn 1969]	[Borror & White 1970]; Richards & Davies 1977	772.

taxon	mouthpart-morphology data	dietary data	no.
SIPHONAPTERA			
Sf. Hystrichopsylloidea			
Coptopsyllidae			
Hystrichopsyllidae			
Anomiopsyllus sp.	Snodgrass 1946	Arnett 1985	773.
Hystrichopsyllus gigas Rothschild	Snodgrass 1946	[Arnett 1985]	774.
Stephanocircidae			
Cleopsylla townsendi Rothschild	Johnson 1957	Johnson 1957	775.
Pygiopsyllidae			
Ctenidiosomus traubi Johnson	Johnson 1957	Johnson 1957	776.
Ctenophthalmidae			
Chimaeropsyllidae			
Sf. Ceratophylloidea			
Ancistropsyllidae			
Xiphiopsyllidae			
Ceratophyllidae			
*Ceratophyllus wickhami** Baker	Sikes 1930; [Johnson 1957]	Sikes 1930	777.
Cratynius crypticus Hopkins & Traub	Hopkins & Traub 1955	Hopkins & Traub 1955	778.
*Leptopsylla pectiniceps** Wagner	Perfiljew 1927	[Swan & Papp 1972]	779.
*Nosopsyllus fasciatus** (Bosc)	Sharif 1937; Elbel 1951	Elbel 1951; Peterson 1951; Arnett 1985	780.
Opisodasys pseudarctomys (Baker)	Snodgrass 1946	[Arnett 1985]	781.
Ischnopsyllidae			
Sternopsylla distincta (Rothschild)	Johnson 1957	Johnson 1957	782.
Sf. Malacopsylloidea			
Malacopsyllidae			
Malacopsylla grossiventris Weyenbergh	Johnson 1957	Johnson 1957	783.
Rhopalopsyllidae			
Rhopalopsyllus lugubris (Enderlein)	Johnson 1957	Johnson 1957	784.
Sf. Vermipsylloidea			
Vermipsyllidae			
Sf. Pulicoidea			
Pulicidae			
Ctenocephalides canis (Curtis)	Packard 1898; Lass 1905; Snodgrass 1944; Wenk 1953; Gouin 1968	Swan & Papp 1972; Arnett & Jacques 1981; Arnett 1985	785.
Ctenocephalides felis (Bouché)	Nitzulescu 1927; Snodgrass 1944, 1946; Johnson 1957	Swan & Papp 1972; Milne & Milne 1980	786.
*Ctenocephalides felis** (Bouché)	Peterson 1951; Elbel 1951	Peterson 1951; Elbel 1951	787.
Echidnophaga gallinacea (Westwood)	Snodgrass 1946; Johnson 1957	Swan & Papp 1972; Arnett 1985	788.

taxon	mouthpart-morphology data	dietary data	no.
Pulex irritans Linneaus	[Crampton 1923a, 1923b]; Tillyard 1935; Snodgrass 1944, 1946; Johnson 1957	Swan & Papp 1972; Milne & Milne 1980; Arnett 1985	789.
Xenopsylla cheopis Rothschild	Rothschild 1906; Johnson 1957	Swan & Papp 1972; Milne & Milne 1980; Arnett 1985	790.
*Xenopsylla cheopis** Rothschild	Sikes 1930	Sikes 1930; Swan & Papp 1972	791.
Tungidae			
Tunga penetrans Linneaus	Johnson 1957	Johnson 1957	792.
DIPTERA			
So. **Nematocera**			
Sf. **Tipuloidea**			
Trichoceridae			
Trichocera bimaculata Walker	Peterson 1916; [Crampton 1942]; [Hoyt 1952]; [Cole 1969]; Alexander 1981b	diet undocumented	793.
*Trichocera** sp.	[Bischoff 1922a]; [Keilin 1940]; Anthon 1943a; Peterson 1951; Kramer 1954; Alexander 1981b; [Smith 1986]	Peterson 1951	794.
Tipulidae			
Dicranomyia sp.	Hoyt 1952	Rogers 1932; [Merritt & Schlinger 1984]	795.
*Dicranota** sp.	Johannsen 1934; Cook 1949	Uvarov 1928; [Byers 1984]	796.
*Eriocera** sp.	Johannsen 1934; Cook 1949	Byers 1984	797.
Erioptera sp.	Crampton 1917b; Hoyt 1952	Rogers 1933; [Merritt & Schlinger 1984]	798.
Geranomyia rufescens	Peterson 1916; Crampton 1942; Hoyt 1952	Rogers 1927; Merritt & Schlinger 1984	799.
*Holorusia rubignosa** Loew	Kellogg 1899; Cook 1949	Uvarov 1928; Rogers 1933; Milne & Milne 1980	800.
Limnophila sp.	Hoyt 1952	Rogers 1926; [Merritt & Schlinger 1984]	801.
*Tipula livida** Van der Wulf	[Das 1938]; [Snodgrass 1947]; [Peterson 1951]; Chiswell 1955; [Teskey 1976]	[Rogers 1926, 1933]; [Arnett & Jacques 1981]; Milne & Milne 1980	802.

taxon	mouthpart-morphology data	dietary data	no.
Tipula reesi Rees & Ferris	[Wesche 1909]; [Meijere 1916]; [Peterson 1916]; Rees & Ferris 1939; [Hoyt 1952]	[Rogers 1926, 1933]; Arnett & Jacques 1980	803.
Sf. Psychodoidea			
Tanyderidae			
Protoplasa fitchii Osten Sachen	Williams 1933; Johannsen 1934	[Merritt & Schlinger 1984]	804.
*Protoplasa fitchii** Osten Sachen	Crampton 1930b; Kramer 1954	Alexander 1981a	805.
Tanyderus forcipatus	Crampton 1942	[Merritt & Schlinger 1984]	806.
Ptychopteridae			
Bittacomorpha clavipes Fabricius	Peterson 1916; Crampton 1917b; 1942	Milne & Milne 1980; [Arnett & Jacques 1981]	807.
*Bittacomorpha clavipes** Fabricius	Kramer 1954	Rogers 1933	808.
Liriope lenis (Osten Sachen)	Hoyt 1952	Rogers 1926, 1933	809.
Ptychoptera rufocincta Osten Sachen	Peterson 1916	Rogers 1926	810.
*Ptychoptera lenis** Osten Sachen	[Bischoff 1922a]; [Johannsen 1934]; [Anthon 1943a]; [Snodgrass 1943]; [Peterson 1951]; [Hodkinson 1973]	Uvarov 1928; Merritt & Schlinger 1984; [Mattingly 1987a]	811.
Psychodidae			
Lutzomyia flaviscutella (Mangabeira)	Lewis 1975; Quate & Vockeroth 1981	[Arnett 1985]	812.
Phlebotomus papatasii Scopoli	[Cragg 1913a]; Alder & Theodor 1926; [Christophers, Shortt & Barraud 1926]; [Shortt & Swaminath 1928]; [Snodgrass 1943, 1944, 1959]; [Iams 1944]; Hennig 1950; [Grenier 1959]; [Lewis 1975]	Swan & Papp 1972	813.
Psychoda albipennis Zetterstedt	[Kellogg 1899]; [Dell 1905]; Peterson 1916; [Anthon 1943a]; Quate & Vockeroth 1981	[Cole 1969]	814.
*Psychoda sexmaculata** Curtis	Dell 1905; [Peterson 1951]	Dell 1905; Swan & Papp 1972; Teskey 1984	815.
Sf. Culicoidea			
Dixidae			
Dixa clavata (Loew)	Peterson 1916; [Iams 1944]; Peters 1981	[Merritt & Schlinger 1984]; [Peters 1981]	816.

taxon	mouthpart-morphology data	dietary data	no.
*Dixa maculata** Meigen	[Smith 1928]; [Johannsen 1934]; Schremmer 1950b; [Peterson 1951]; [Felix 1962]; [Chaudonneret 1963]; [Knight 1971]; Peters 1981	Peterson 1951; Teskey 1984	817.
Chaoboridae			
*Australomochlonyx nitidus** Freeman	Colless 1977; Cook 1981	Colless 1977	818.
Corethella appendiculata Grabhan	McKeever 1986	Cook 1981; McKeever 1986	819.
*Eucorethra underwoodi** Underwood	Johannsen 1934; Peterson 1951; Knight 1971	Peterson 1951	820.
Culicidae			
Aedes aegypti (Linneaus)	[Williston 1908]; Snodgrass 1944, 1959; [Hoyt 1952]; [Hudson 1970]; Davies 1971; Wenk 1980; Stone 1981; Ross *et al.* 1982	Swan & Papp 1972; [Arnett & Jacques 1981]	821.
*Aedes communis** (DeGeer)	[DuPorte 1946]; [Shalaby 1957a]; [Pao & Knight 1970]; [Knight 1971]; Gardner & Nielsen 1973; Gardner, Nielsen & Knight 1973; [Harbach 1977]; [Manning 1978]; Newson 1984; [Aly 1984]; Dahl *et al.* 1988	Milne & Milne 1980; [Arnett & Jacques 1981]; Dahl *et al.*	822.
Anopheles maculipennis Meigen	[Kulagin 1905]; [Cragg 1913a]; Vogel 1921; Sinton & Covell 1927; Barraud & Covell 1928; Robinson 1939; [Crampton 1942]; Snodgrass 1943; Wenk 1961, 1980	Swan & Papp 1972; [Arnett & Jacques 1981]	823.
*Anopheles quadrimaculatus** Say	[Johannsen 1934]; [Cook 1944b]; Farnsworth 1947; Hennig 1950; [Schremmer 1950a]; Shalaby 1956; Menees 1958a, 1958b; Snodgrass 1959; [Knight 1971]; [Harback 1977]; Stone 1981	[Peterson 1951]; Pucat 1965; Swan & Papp 1972	824.
*Armigeris malayi** Theobald	Cook 1944b; [Knight 1971]; [Harbach 1977, 1978]	McCafferty & Provonsha 1983]	825.
Culex pipiens Linneaus	[Dimmock 1881]; [Kellog 1899]; Wesche 1902, 1904, 1909; Kulagin 1905; [Barraud & Covell 1928]	Swan & Papp 1972; Milne & Milne 1980; Arnett 1985	826.
*Culex pipiens** Linneaus	Bischoff 1922a; Johannsen 1934; Chaudonneret 1951, 1962, 1963; [Shalaby 1957b]; Snodgrass 1959; [Knight 1971]; Harbach 1977, 1978; Dahl et al. 1988	Newson 1984; Dahl *et al.* 1988	827.

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
241.	Archaeolepidae: *Archaeolepis mane* Whalley	[69]	Whalley 1985; 1986
242.	Micropterygidae: *Parasabatinca aftimacrai* Whalley	[55]	Whalley 1978; 1986
243.	Micropterygidae: *Palaeosabatinca zherichini* Kozlov	[52]	Kozlov 1988b
244.	Unnamed micropterygid	[45]	Schlüter 1975, 1978
245.	Micropterygidae: *Sabatinca proavitella* Rebel	[19]	Rebel 1935; Larsson 1978
246.	Micropterygidae: *Micropteryx angelica* Jarzembowski	[18]	Jarzembowski 1980
247.	?Eriocraniidae: *Undopteryx sukatshevi* Skalski	[52]	Skalski 1979a; Whalley 1986
248.	"Lophocoronid-like specimen"	[37]	Skalski 1979b
249.	"Incurvariine type"	[55]	Whalley 1977, Hennig 1981

MOUTHPART CLASS 5: MAXILLOLABIATE

Fig. 43

1.	Megaspilidae: *Allocotidus bruesi* Muesebeck	[40]	Muesebeck 1963
2.	Maimetshidae: *Maimetsha arctica* Rasnitsyn	[37]	Rasnitsyn 1975
3.	Stigmaphronidae: *Lygocerus(?) dubiatus* Brues	[35]	Masner & Dessart 1967
4.	Calliceratidae: *Conostigmus succinalis* Brues	[19]	Brues 1940b
5.	Heloridae: *Protohelorus mesozoicus* Kozlov, Proctotrupidae: *Mesoserphus karatavicus* Kozlov, Monomachidae, Diapriidae	[60]	Martynov 1925, Kozlov 1968
6.	"Proctotrupid indet."	[53]	Jell & Duncan 1986
7.	Pelecinidae: *Iscopinus baissicus* Kozlov	[52]	Kozlov 1974
8.	Scelionidae: *Cenomanioscelio pulcher* Schlüter, Diapriidae: Ismarinae	[45]	Schlüter 1978
9.	Scelionidae, ?Vanhorniidae, Diapriidae, Serphitidae	[37]	Zherikin & Sukacheva 1973
10.	Serphitidae: *Serphites paradoxus* Brues, Scelionidae: *Proteroscelio antennalis* Brues, ?Vanhorniidae	[35]	Brues 1937, McAlpine & Martin 1969
11.	Proctotrupidae: *Cryptoserphus pivorus* Brues, Scelionidae: *Pelecinopteron tubuliforme* Brues, Diapriidae: *Ambositra* sp.	[19]	Brues 1933, 1940a; Masner 1969
12.	Diapriidae: *Galesimorpha wheeleri* Brues, Belytidae: *Belyta mortuella* Brues	[15]	Brues 1910
13.	Scelionidae: *Palaegyron muesbecki* Masner	[11]	Masner 1969
14.	Scelionidae: *Platygasterites femoralis* Statz, Heloridae: *Helorus festivus* Statz 1938	[8]	Statz 1938
15.	Mymaridae: *Galloromma bezonnaisensis* Schlüter	[45]	Schlüter 1978
16.	Eulophidae	[40]	Lagenheim *et al.* 1960
17.	Mymaridae, Chalcidoidea	[37]	Zherikin & Sukacheva 1973; Rasnitsyn 1975
18.	Trichogrammatidae: *Enneagmus pristinus* Yoshimoto, Tetracampidae: *Distylopus bisegmentatus* Yoshimoto, Mymaridae: *Triadomerus bulbosus* Yoshimoto	[35]	Yoshimoto 1975
19.	"Possibly an encyrtid chalcidoid"	[33]	George 1952
20.	Mymaridae	[25]	Saunders *et al.* 1974
21.	Chalcidoidea: *Arescon armata* (Meunier)	[19]	Meunier 1905a

(MAXILLOLABIATE, continued)

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
22.	Agaonidae	[15]	Brues 1910
23.	Chalcidoidea	[8]	Statz 1938
24.	Cynipidae	[37]	Zherikin & Sukacheva 1973
25.	Cynipidae: *Protimaspis costalis* Kinsey	[35]	Kinsey 1937
26.	Cynipidae: *Aulacidea succinea* Kinsey	[19]	Kinsey 1919
27.	Cynipidae: *Rhodites vetus* Cockerell	[18]	Cockerell 1921
28.	Ibalidae: *Protoabalia connexiva* Brues, Figitidae: *Gigites solus* Brues	[15]	Brues 1910
29.	Cynipoidea	[8]	Statz 1938
30.	Aulacidae: *Mesaulacinus oviformis* Martynov	[60]	Martynov 1925
31.	Aulacidae: *Paraulacus sinicus* Ping	[L. Jura]	Ping 1928
32.	Cretevaniidae	[57]	Jarzembowski 1984
33.	Cretevaniidae: *Cretevania minuta* Rasnitsyn, Aulacidae: *Mesaulacinus* sp., ?Trigonalyidae: Cleistogastrinae	[37]	Zherikin & Sukacheva 1973; Rasnitsyn 1981
34.	Evaniidae: *Evania remanea* Brues	[19]	Brues 1933
35.	Aulacidae: *Micraulacinus prisculus* Brues, Evaniidae: *Pristaulacus rohweri* Brues, Praeaulacidae	[15]	Brues 1910; Rasnitsyn 1972
36.	?Bethyloid indet.	[53]	Jell & Duncan 1986
37.	Dryinidae: *Cretodryinus zherichini* Ponomarenko, Chrysididae: *Hypocleptes rasnitsyni* Evans, Scolebythidae: *Cretabythus sibiricus* Evans, Bethylidae: *Archepyris minutus* Evans	[37]	Evans 1973, Rasnitsyn 1975
38.	Chrysididae: *Procleptes carpentieri* Evans	[35]	Evans 1969
39.	Chrysididae: *Protochrysis succinalis* Bischoff, Embolemidae: *Embolemus breviscaptus* Brues	[19]	Bischoff 1915; Brues 1933
40.	Chrysididae: ?*Epyris tenellus* Statz	[8]	Statz 1938
41.	Pompilidae: *Pompiliopterus ciliatus* Rasnitsyn	[52]	Rasnitsyn 1975
42.	Pompilidae: *Epipompilius* sp.	[19]	Köningsmann 1978b
43.	Pompilidae: *Psammochares* sp.	[8]	Statz 1936, 1938
44.	Mutillidae: *Cretavus sibiricus* Sharov	[Cenoman]	Sharov 1957a; Hennig 1981
45.	Tiphiidae	[37]	Zherikin & Sukacheva 1973
46.	Mutillidae: *Protomutilla* sp., Sapygidae	[19]	Bischoff 1927; Brothers 1974
47.	Tiphiidae: *Geotiphia* sp.	[15]	Handlirsch 1908
48.	Angarosphecidae: *Angarosphex myrmicopterus* Rasnitsyn	[52]	Rasnitsyn 1975
49.	Falsiformicidae: Species A	[45]	Rasnitsyn 1975
50.	Falsiformicidae: *Falsiformica cretacea* Rasnitsyn	[37]	Rasnitsyn 1975
51.	Masaridae: *Curiovespa curiosa* Rasnitsyn	[39]	Rasnitsyn 1975
52.	Eumenidae	[27]	Piton 1940; Burnham 1978
53.	Vespidae: *Palaeovespa baltica* Cockerell	[19]	Cockerell 1909e
54.	Vespidae: *Polistes industrius* Théobald, Eumenidae: *Rhynchium* sp.	[13]	The'obald 1937
55.	Eumenidae: *Alastor rottensis* Statz, Vespidae: *Vespa nigra* Statz	[8]	Statz 1936
56.	Formicidae	[55]	Hennig 1981
57.	Formicidae: *Cretacoformica explicata* Jell & Duncan	[53]	Jell & Duncan 1986

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
*Bibio** sp.	Kellogg 1899; [Bischoff 1922a]; Das 1938; Cook 1944a, 1949; Snodgrass 1947; Hoyt 1952; Perraudin 1961; Teskey 1976; Hardy 1981	Swan & Papp 1972; Cole 1969	857.
Scatopsidae			
Hyperoscelidae			
*Synneuron decipiens** Hutson	Mamayev & Krivosheina 1969; [Teskey 1976]; [Peterson & Cook 1981]	[Teskey 1976]; Peterson & Cook 1981	858.
Cecidomyiidae			
*Clinodiplosis cilicrus** Kieffer	Otter 1938	Otter 1938	859.
*Dasyneura miki** Kieffer	Otter 1938; [Teskey 1976]; [Gagné 1981]	Otter 1938; [Swan & Papp 1972]	860.
*Lestodiplosis miki** Barnes	Otter 1938; [Hennig 1948]	Otter 1938	861.
*Phaenobremia aphidimyza** (Rondani)	Solinas 1968	[Clausen 1940]	862.
Rhabdophaga strobiloides (Osten Sacken)	Peterson 1916	[Cole 1969]	863.
Sciaridae			
Sciara varians	[Frey 1913]; Peterson 1916; Steffan 1981	Cole 1969	864.
*Sciara** sp.	[Bischoff 1922a]; Snodgrass 1947; Peterson 1951; [Perraudin 1961]	Cole 1969; Teskey 1976	865.
Mycetophilidae			
*Epidapus scabiei** Hopkins	Hopkins 1896	Hopkins 1896	866.
Mycetophila divergens Walker	[Frey 1913]; Peterson 1916; Vockeroth 1981	Milne & Milne 1980	867.
Incertae Sedis			
Blepharoceridae			
Agathon sp.	Ferris 1942; Hogue 1981	[Cole 1969]; [Hogue 1981]	868.
Bibiocephala elegantula Roder	[Kellogg 1899]; Peterson 1916	[Hogue 1981]	869.
Edwardsina sp.	Crampton 1923, 1942; [Imms 1944]; Hogue 1981	[Hogue 1981]	870.
Liponeura cinerascens Bischoff	[Kellogg 1899]; Pryor 1948	[Hogue 1981]	871.
Deuterophlebiidae			
*Deuterophlebia inyoensis** Kennedy	Kennedy [1958], 1960, [1981]	Kennedy 1960; Merritt & Schlinger 1984	872.
Nymphiomyiidae			
Nymphomyia alba Tokunaga	Tokunaga 1932, 1935; Rohdendorf & Kalugina 1974	Tokunaga 1935; Kevan & Cutten 1981	873.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
So. Brachycera			
Io. Orthorrhapha			
Sf. Tabanoidea			
Pelecorhynchidae			
*Glutops rossi** Pechuman	Teskey 1970, 1981a	Teskey 1981a; Merritt & Schlinger 1984	874.
Rhagionidae			
Chrysopilus auratus Fabricius	Wesche 1909; Chassignard & Tsacas 1974	[Milne & Milne 1980]	875.
*Chrysopilus** sp.	Greene 1926; Peterson 1951; [Schremmer 1952]; Gouin 1968; [James & Turner 1981]	Greene 1926; Clausen 1940; Peterson 1951	876.
*Rhagio scolopaceus** (Linneaus)	Schremmer 1952; Gouin 1968; Roberts 1969; James & Turner 1981	Roberts 1969	877.
Rhagio vertebratus (Say)	Peterson 1916; [Hoyt 1952]; [Bletchly 1955]	Bletchley 1955; [Arnett & Jacques 1981]	878.
Symphoromyia atripes Bigot	[Williston 1908]; Snodgrass 1943, 1944; [Hoyt 1952]; Ross 1965, 1982; [James & Turner 1981]	Swan & Papp 1972; Waage 1979	879.
Vermileo vermileo DeGeer	Chassagnard & Tsacas 1974; [Teskey 1981c]	[Swan & Papp 1972]	880.
Athericidae			
Xylophagidae			
*Xylophagus abdominalis** Loew	[Bischoff 1924]; Greene 1926; [Teskey 1976]; [James 1981a]	Greene 1926; Teskey 1976	881.
Stratiomyidae			
*Chloromyia formosa** Scopoli	Vaillant & Delhom 1956	[Arnett & Jacques 1981]; [McCafferty & Provonsha 1983]	882.
*Hermetia illucens** Linneaus	Peterson 1951; [James 1981b]; Smith 1986	Peterson 1951; Arnett 1985	883.
*Odontomyia limbata** (Meigen)	[Cook 1949]; [Peterson 1951]; Hennig 1952; Vaillant & Delhom 1956; [James 1981b]	Vaillant & Delhom 1956; Merritt & Schlinger 1984	884.
*Oxycera pygmaea** (Fallen)	Vaillant & Delhom 1956	Vaillant & Delhom 1956	885.
*Sargus bipunctatus** Scopoli	[Bischoff 1924]; [Peterson 1951]; Roberts 1969; [James 1981b]	[Peterson 1951]; Roberts 1984; Merritt & Schlinger	886.
Stratiomys apiculata	Peterson 1916; [Hu & Feng 1936]; [James 1981b]	[Arnett 1985]	887.

taxon	mouthpart-morphology data	dietary data	no.
*Stratiomys chamaeleon** Linneaus	[Peterson 1951]; Schremmer 1952	Peterson 1951; Arnett 1985	888.
Tabanidae			
Chrysops vittatus Wiedemann	Smith 1898; Lall & Davies 1971; [Pechuman & Teskey 1981]; [Suvarova 1985]	Lall & Davies 1971; [Kniepert 1980]	889.
Corizoneura longirostris Hardwick	Waterhouse 1893; Mitter 1918; Tetley 1918; Crampton 1923b; [Nitzulescu 1927a]; [Zaitsev 1982]	Mitter 1918; Tetley 1918	890.
Haematopota pluvialis (Meigen)	Wesche 1902, 1904; Cragg 1912a 1913a, 1913c; [Wenk 1962, 1980]; Suvarova 1985	Cragg 1913c; Kniepert 1980	891.
*Tabanus atratus** Fabricius	Peterson 1951; Pechuman & Teskey 1981	[Clausen 1940]; Peterson 1951; Swan & Papp 1972	892.
Tabanus giganteus	[Packard 1898]; [Smith 1890]; Peterson 1916; [Lindner 1919]; [Snodgrass 1935, 1944]; [Crampton 1942]; [Snodgrass 1944]; [Imms 1944]; [Bonhag 1951]; [Grenier 1959]; [Atkins 1978]; [Stoffolano & Yin 1983]; [Chaudonneret 1989b]	[Kniepert 1980]; [Arnett & Jacques 1981]; [McCafferty & Provonsha 1981]; Stoffolano & Yin 1983	893.
Pantophthalmidae			
Pantophthalmus comptus Enderlein	Val 1976	Val 1976; [Bickel 1982]	894.
Nemestrinidae			
*Neorhynchocephalus sulphureus** (Wiedemann)	Crouzel & Salavin 1943	Crouzel & Salavin 1943	895.
Acroceridae			
Lasia sp.	[Williston 1908]; Crampton 1942; [Schlinger 1981]	Schlinger 1981	896.
Ogcodes costatus Loew	Williston 1908; Peterson 1916; [Crampton 1942]; Cole 1969; [Schlinger 1981]	[Clausen 1940]; [Schlinger 1981]	897.
Sf. Asiloidea			
Asilidae			
Dioctria aldbius Walker	Hoyt 1952; Cole 1969; [Wood 1981c]	[Cole 1969]; Whitfield 1925	898.
*Laphria** sp.	[Bischoff 1924]; Peterson 1951; [Hennig 1952]; Teskey 1976; [Wood 1981c]	[Peterson 1951]; [Wood 1981c]	899.
Machimus atricapillus Fallén	Packard 1898; Whitfield 1925; Snodgrass 1943, 1944	[Poulton 1906]; Whitfield 1925	900.
Proctacanthus sp.	Snodgrass 1943, 1944	Poulton 1906; Clausen 1940; Milne & Milne 1980	901.

taxon	mouthpart-morphology data	dietary data	no.
Promachus vertebratus (Say)	Peterson 1916	Poulton 1906; Swan & Papp 1972	902.
*Promachus vertebratus** (Say)	Peterson 1951; [Wood 1981c]	[Poulton 1906]; Peterson 1951; Milne & Milne 1980	903.
Mydidae			
Mydas clavatus (Drury)	Peterson 1916; Wilcox 1981; Zaitlin & Larsen 1984	Swan & Papp 1972; Arnett & Jacques 1981	904.
*Mydas clavatus** (Drury)	Peterson 1951; Teskey 1976; Wilcox 1981	Teskey 1976; Wilcox 1981	905.
Therevidae			
Psilocephala haemorrhoidalis (Marquart)	Peterson 1916	Arnett 1985	906.
*Thereva furcata** Loew	[Hennig 1952]; Irwin & Lyneborg 1981]	[Peterson 1951]; Irwin & Lyneborg 1981	907.
Scenopinidae			
Scenopinus fenestralis (Linneaus)	[Williston 1908]; Peterson 1916; Kelsey 1981	Swan & Papp 1972; Arnett &	908.
Bombyliidae			
Exoprosopa fasciata Macquart	Peterson 1916	[Swan & Papp 1972]; Milne & Milne 1980	909.
*Toxophora virg*ata Osten Sacken	Hoyt 1952	[Swan & Papp 1972]	910.
Apioceridae			
*Apiocera maritima** Hardy	English 1947; Peterson 1981c	English 1947	911.
Sf. **Empidoidea**			
Empididae			
*Empis livid*a Linneaus	[Smith 1898]; [Wesche 1902, 1904, 1909]; [Peterson 1916]; Crampton 1923; Bletchly 1954; Kristoph 1961; [Steyskal & Knutson 1981]	Poulton 1906; [Clausen 1940]	912.
*Hemerodromia** sp.	Bischoff 1924; Steyskal & Knutson 1981	[Richards & Davies 1977]; Merritt & Schlinger 1984	913.
Dolichopodidae			
Dolichopus bifractus Loew	[Wesche 1909]; Peterson 1916; Cregan 1941; [Robinson & Vockeroth 1981]	Cregan 1941; [Swan & Papp 1972]	914.
*Dolichopus ramifer** Loew	Peterson 1951	Peterson 1951; Swan & Papp 1972; Merritt & Schlinger 1984	915.
*Medeterea** sp.	Hennig 1952; Robinson & Vockeroth 1981	Hennig 1952	916.
*Melanderia mandibul*ata Aldrich	Aldrich 1922; Snodgrass 1922a; Cregan 1941; [Robinson & Vockeroth 1981]	Cregan 1941; Richards & Davies 1977	917.

taxon	mouthpart-morphology data	dietary data	no.
*Systenus albimanus** Wirth	Wirth 1952	Wirth 1952; Merritt & Schlinger 1984	918.
Io. Cyclorrhapha			
Div. Aschiza			
Sf. Lonchopteroidea			
Lonchopteridae			
Lonchoptera lutea Panzer	[Wesche 1909]; Peterson 1916	[Wesche 1909]	919.
Sf. Phoroidea			
Platypezidae			
Platypeza velutina	[Wesche 1909]; Peterson 1916	[Wesche 1909]	920.
Ironomyiidae			
Ironomyia nigromaculata White	McAlpine 1967	diet undocumented	921.
Sciadoceridae			
*Sciadocera rufomaculata** White	Fuller 1934	Fuller 1934	922.
Phoridae			
Megaselia agarici	Peterson 1916; Oldroyd 1964; [Elzinga & Broce 1986]; [Smith 1986]	Clausen 1940; Swan & Papp 1972	923.
Phora curvinervis Becker	Wesche 1909	[Cole 1969]	924.
Sf. Syrphoidea			
Syrphidae			
Eristalis arbustorum Linneaus	[Smith 1890]; [Wesche 1904]; [Peterson 1916]; Schiemenz 1957; [Holloway 1976]; [Gilbert 1981]; [Zaitsev 1982]; [Schuhmacher & Hoffman 1982]; [Elzinga & Broce 1986]	[Arnett & Jacques 1981]	925.
*Eristalis tenax** (Linneaus)	[Peterson 1951]; Hartley 1963; Teskey 1984	Peterson 1951; Oldroyd 1964; Swan & Papp 1972	926.
*Eumerus strigatus** Fallen	Hennig 1952; Roberts 1970	Roberts 1970	927.
*Myanthropea florea** (Linneaus)	Roberts 1970	Roberts 1970	928.
Rhingia nasica Say	Crampton 1942; Curran 1965; [Gilbert 1981]; [Vockeroth & Peterson 1981]; [Schuhmacher & Hoffmann 1982]	Oldroyd 1964; Gilbert 1981; Arnett 1985	929.
Pipunculidae			
Pipunculus cingulatus Loew	Peterson 1916; Cole 1969	Oldroyd 1964; [Cole 1969]	930.
Div. Schizophora			
Sf. Conopoidea			
Conopidae			
Conops brachyrhynchus (Macquart)	[Williston 1908]; Peterson 1916; [Frey 1921]	[Clausen 1940]; Elzinga & Broce 1987	931.
Sf. Tephritoidea			
Tephritidae			
Euaresta aequalis (Loew)	Peterson 1916; [Elzinga & Broce 1986]	[Curran 1965]; Elzinga & Broce 1986	932.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
_Toxotrypana curvicauda_* Gerstaecker	Greene 1929	Greene 1929	933.
Otitidae			
Physiphora demandata (Fabricius)	Peterson 1916; Elzinga & Broce 1986	Cole 1969; Elzinga & Broce 1986	934.
_Tritoxa incurva_* Loew	Allen & Foote 1975	Allen & Foote 1975	935.
_Eumetopia rufipes_* (Marquart)	Valley, Novak & Foote 1969	Valley, Novak & Foote 1969	936.
Platystomatidae			
Platystoma seminationis Linneaus	Frey 1921	[Cole 1969]	937.
Pyrgotidae			
Tachiniscidae			
Richardiidae			
Ozaenina diversa	Oldroyd 1964	[Cole 1969]	938.
Pallopteridae			
Palloptera saltum Linneaus	Frey 1921; [Cole 1969]	[Curran 1965]	939.
Piophilidae			
_Piophila casei_* Linneaus	Wille 1922; [Smith 1986]	Wille 1922; Arnett 1985	940.
_Neottiophilum praeustum_* Meigen	Tate 1954	Tate 1954	941.
Lonchaeidae			
_Lonchaea chorea_* Fabricius	Cameron 1913; [Hennig 1935]; [Teskey 1976]	Cameron 1913; [Teskey 1976]	942.
Sf. Micropezoidea			
Cypselosomatidae			
_Cypselosoma australis_* McAlpine	McAlpine 1966	McAlpine 1966	943.
Pseudopomyzidae			
Pseudomyza atrimana Meigen	Krivosheina 1979	diet undocumented	944.
Neriidae			
Glyphidops filosus	Crampton 1942; Aczel 1961	diet undocumented	945.
Micropezidae			
Compsobata univitta (Walker)	Peterson 1916; [Frey 1921]	Oldroyd 1964	946.
Megamerinidae			
Sf. Tanypezoidea			
Nothybidae			
Nothybus longithorax Rondani	Aczel 1955	Aczel 1955	947.
Diopsidae			
Sphyracephala brevicornis Say	Peterson 1916; Cole 1969; Elzinga & Broce 1986	Oldroyd 1964; Elzinga & Broce 1986	948.
Teleopsis bigoti Hendel	[Crampton 1942]; Cole 1969	[Oldroyd 1964]	949.
Tanypezidae			
_Tanypeza longimana_* Fallen	Foote 1970	Foote 1970	950.
Psilidae			
Loxocera pectoralis	[Williston 1908]; Peterson 1916; [Elzinga & Broce 1986]	[Hennig 1965]	951.
Syringogastridae			
Strongylophthalmyiidae			

taxon	mouthpart-morphology data	dietary data	no.
Sf. Sciomyzoidea			
Heliomyzidae			
Dryomyzidae			
*Dryomyza analis** Fallen	Smith 1986b; Steyskal 1987	Smith 1986b	952.
Coelopidae			
Coelopa vanduzeii Cresson	Williston 1908; Peterson 1916; [Frey 1921]	Milne & Milne 1980	953.
Sciomyzidae			
Tetanocera plumosa Loew	Williston 1908; Peterson 1916; [Frey 1921]; Elzinga & Broce 1986	Milne & Milne 1980; Elzinga & Broce 1986	954.
Chamaemyiidae			
*Leucopis verticalis** Malloch	[Hennig 1952]; Sluss & Foote 1971; Teskey 1976	Teskey 1976	955.
Ochthiphila juncorum Fallen	Williston 1908; Frey 1921	Oldroyd 1964	956.
Ropalomeridae			
Ropalomera pleuropunctata Wiedemann	Williston 1908; Frey 1921	Arnett 1985	957.
Sepsidae			
Sepsis violacea Meigen	[Williston 1908]; Peterson 1916; [Frey 1921]; Hoyt 1952; [Elzinga & Broce 1986]; [Smith 1986]	[Cole 1969]; Elzinga & Broce 1986	958.
Lauxaniidae			
Sapromyza vulgaris	Peterson 1916; [Frey 1921]; [Broadhead 1984]	[Broadhead 1984]; [Arnett 1985]	959.
Celyphidae			
Spaniocelyphus scutatus Wiedemann	Frey 1921	diet undocumented	960.
Sf. Opomyzoidea			
Opomyzidae			
Opomyza florum Fabricius	Frey 1921; Cole 1969; [Vockeroth 1987a]	[Cole 1969]	961.
*Opomyza germationis** Linneaus	Thomas [1933], 1934	Thomas 1934	962.
Clusiidae			
Clusiodes convergens Malloch	Peterson 1916	[Cole 1969]	963.
Acartophthalmidae			
Sf. Agromyzoidea			
Odiniidae			
*Neoalticomerus seamansii** Shewell	Shewell 1960	Shewell 1960; [Arnett 1985]	964.
Agromyzidae			
Agromyza sp.	Williston 1908; Frey 1921	[Arnett 1985]; [Elzinga & Broce 1986]	965.
Fergusoninidae			
*Fergusonia tillyardi** Tonnoir	Currie 1937	Currie 1937	966.
Sf. Asteioidea			
Neurochaetidae			
Neurochaeta inversa McAlpine	McAlpine 1978	McAlpine 1978	967.
Periscelidae			
Periscelis annulipes Loew	Duda 1934a; McAlpine 1987a	Oldroyd 1964; McAlpine 1987a	968.
Teratomyzidae			

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
Aulacigastridae			
*Aulacigaster leucopeza** (Meigen)	Robinson 1953; Teskey 1976, 1987	Teskey 1976	969.
Asteiidae			
Asteia concinna Meigen	Duda 1934b	[Cole 1969]; [Sabrosky 1981]	970.
Anthomyziidae			
Anthomyza gracilis Fallen	Frey 1921; Cole 1969; Vockeroth 1987b	[Cole 1969]	971.
Rhinotoridae			
Sf. Drosophiloidea			
Drosophilidae			
Drosophila melanogaster Meigen	[Williston 1908]; [Peterson 1916]; [Frey 1921]; [Smith 1926]; Hoyt 1952; Ross 1982; Smith 1986	Swan & Papp 1972; Milne & Milne 1980; Arnett & Jacques 1981	972.
Mystacinobiidae			
Mystacinobia zelandica Holloway	Holloway 1976	Holloway 1976	973.
Camillidae			
Camilla glabra Fallen	Frey 1921	Olroyd 1964	974.
Ephydridae			
Dichaeta caudata Fallen	Frey 1921; [Cole 1969]	Swan & Papp 1972	975.
Ochthera mantis (DeGeer)	[Williston 1908]; Peterson 1916	McCafferty & Provonsha 1983; Cole 1969	976.
Diastatidae			
Diastata nebulosa Fallen	Duda 1934d; McAlpine 1987c	diet undocumented	977.
Curtonotidae			
Curtonotum anus Meigen	Duda 1934c; McAlpine 1987b	diet undocumented	978.
Sf. Chloropoidea			
Chloropidae			
Chlorops taeniopus Meigen	Frey 1921; Frew 1923	[Cole 1969]	979.
Thaumatomyia glabra (Meigen)	Peterson 1916; Elzinga & Broce 1986	Swan & Papp 1972; Cole 1969; Elzinga & Broce 1986	980.
Milichiidae			
Desmometopa latipes (Meigen)	[Williston 1908]; Peterson 1916; Frey 1921	Clausen 1940; Elzinga & Broce 1986	981.
Carnidae			
Neomeconeurites chilensis Hennig	Hennig 1972	[Bickel 1982]	982.
Tethinidae			
Tethinia illota Haliday	Frey 1921; Cole 1969	[Cole 1969]	983.
Canaceidae			
*Canace macateei** Malloch	Teskey 1984; Wirth 1987	Teskey 1984	984.
Sf. Muscoidea			
Scatophagidae			
Scatophaga furcata (Say)	Peterson 1916; Elzinga & Broce 1986; [Smith 1986]	[Poulton 1906]; Milne & Milne 1980	985.
Scopeuma stercoraria (Linneaus)	Bletchley 1953	Poulton 1906; Clausen 1940	986.

taxon	mouthpart-morphology data	dietary data	no.
Mormotomyiidae			
*Mormotomyia hirsuta** Austen	Emden 1950; Austen 1936	Emden 1950	987.
Gasterophilidae			
Gasterophilus intestinalis DeGeer	Peterson 1916; Cole 1969	Oldroyd 1964	988.
*Gasterophilus nasalis** Linneaus	Peterson 1951	Peterson 1951; Swan & Papp 1972	989.
Anthomyiidae			
Anthomyia radicum Linneaus	Williston 1908; [Lindner 1919]; Seamans 1920; [Huckett 1987]	Clausen 1940; Swan & Papp 1972	990.
Hydrotaea dentipes (Fabricius)	Peterson 1916; Makhan'ko 1973; Elzinga & Broce 1986; [Smith 1986]	Cole 1969	991.
*Hylemya alcathoe** (Walker)	Teskey [1976], 1981d	[Swan & Papp 1972]	992.
Muscidae			
Fannia scalaris (Fabricius)	Chillcott 1960; Smith 1986	Chillcott 1960	993.
Haematobia irritans (Linneaus)	Cragg 1913c; Patton & Cragg 1913; Cole 1969; Paysinger *et al.* 1978; [Elzinga & Broce 1986]	Swan & Papp 1972; Arnett 1985	994.
Lyperosia minuta Bezzi	Cragg 1913b; Patton & Cragg 1913	Cragg 1913b	995.
Musca domestica Linneaus	Kraepelin 1883; Berlese 1909; Peterson 1916; Patton 1933; Snodgrass 1935, 1943; Crampton 1942; Metcalf, Flint & Metcalf 1962; Ross 1965; Broce & Elzinga 1984; Elzinga & Broce 1986	Uvarov 1928; Swan & Papp 1972;; Milne & Milne 1980; Arnett & Jacques 1981	996.
*Musca domestica** Linneaus	[Holmgren 1904]; Peterson 1951; Swan & Papp 1972; Smith 1986	Peterson 1951; Swan & Papp 1972	997.
Phaonia mirabilis	Schremmer 1956	Schremmer 1956	998.
Stomoxys calcitrans Linneaus	Smith 1898; Hansen 1903; Stephens & Newstead 1907; [Cragg 1913c]; Peterson 1916; Snodgrass 1943, 1944; Gouin 1968; Atkins 1978; McAlpine 1981; Elzinga & Broce 1986; Chaudonneret 1989b	Cole 1969; Waage 1979	999.
Calliphoridae			
Calliphora erythrocephala Linneaus	[Suffolk 1869]; [Macloskie 1884]; [Smith 1890]; [Wesche 1904]; [Berlese 1909]; Graham-Smith 1911, 1930; Snodgrass 1935, [1960]; [Zaitsev 1982]; Smith 1985; [Elzinga & Broce 1986]	Swan & Papp 1972; Milne & Milne 1980	1000.

taxon	mouthpart-morphology data	dietary data	no.
*Calliphora erythrocephala** Linneaus	Wesche 1908; [Miller 1932]; Ludwig 1949; Hennig 1952; [Smith 1986]	Swan & Papp 1972	1001.
*Cochliomyia macellaria** Fabricius	Snodgrass 1953; Smith 1986	Swan & Papp 1972; Arnett 1985	1002.
Lucilia sericata Meigen	[Smith 1890]; Hu & Feng 1936; Menees 1962	Arnett 1985	1003.
*Phormia regina** (Meigen)	Teskey 1981c	Swan & Papp 1972	1004.
Sarcophagidae			
Sarcophaga haemorrhoidalis (Fallen)	Peterson 1916; [Meijere 1916]; [Snodgrass 1960]	Arnett & Jacques 1981	1005.
Wohlfahrtia vigil (Walker)	Downes 1963; Cole 1969; Shewell 1987	Swan & Papp 1972	1006.
Tachinidae			
Archytas analis (Fabricius)	Williston 1908; Peterson 1916; Smith 1985	[McAlpine 1981]	1007.
Thelaira leucozona (Panzer)	Williston 1908; Peterson 1916	[McAlpine 1981]	1008.
Rhinophoridae			
Cuterebridae			
Cuterebra emasculator Fitch	Bennett 1955; Wood 1987	Bennett 1955	1009.
Oestridae			
*Cephenemyia auribarbus** Meigen	Cameron 1932	Cameron 1932	1010.
Glossinidae			
Glossina palpialis Robineau-Desvoidy	[Hansen 1903]; [Patton & Cragg 1913]; Jobling 1933; Snodgrass 1943, 1944; [Gordon *et al.* 1956]; [Popham & Abdillahi 1975]; [Smith 1985]; Elzinga & Broce 1986	Brues 1972; Oldroyd 1964	1011.
Hippoboscidae			
Hippobosca maculata Leach	Patton & Cragg 1913; [Jobling 1926]; Dogra 1967	[Cole 1969]	1012.
Lychnia maura Bigot	Jobling 1926; [Snodgrass 1943]	Cole 1969; Swan & Papp 1972	1013.
Melophagus ovinus Linneaus	Jobling 1926; Snodgrass 1943, 1944; Elzinga & Broce 1986	Swan & Papp 1972; Waage 1979; Milne & Milne 1980	1014.
Olfersia ardeae Marquardt	[Smith 1898]; Peterson 1916; [Maa & Peterson 1987]	Cole 1969	1015.
Streblidae			
Nycteribosca amboinensis Rondani	Jobling 1929	Downes 1971; Waage 1979	1016.
Raymondia lobulata Speiser	Jobling 1929	Downes 1971; Waage 1979	1017.

taxon	mouthpart-morphology data	dietary data	no.
Strebla vespertilionis Fabricius	Jobling 1929; Cole 1969	Downes 1971; Waage 1979	1018.
Trichobius major Coquillet	[Jobling 1929]; Zeve & Howell 1962; [Elzinga & Broce 1986]	Downes 1971; Waage 1979	1019.
Nycteribiidae			
Cyclopodia sykesi Westwood	Jobling 1928a; Crampton 1942	Oldroyd 1964; Downes 1971	1020.
Incertae Sedis			
Heleomyzidae			
Aecothea fenestralis (Fallén)	Peterson 1916	[Elzinga & Broce 1986]	1021.
*Heleomyza serrata** Linneaus	Lobanov 1970	[Arnett 1985]	1022.
Sphaeroceridae			
Borborus equinus (Meigen)	Peterson 1916; Frey 1921	[Cole 1969]; [Elzinga & Broce 1986]	1023.
Leptocera fontinalis (Fallen)	Frey 1921; Kim & Cook 1966; Elzinga & Broce 1986	[Cole 1969]; Elzinga & Broce 1986	1024.
Sphaerocera curvipes Latreille	[Wesche 1904]; [Frey 1921]; Kim & Cook 1966; Elzinga & Broce 1986	[Cole 1969]; Elzinga & Broce 1986	1025.
Chyromyidae			
Gymnochyromya concolor (Malloch)	Peterson 1916; [Frey 1921]	[Cole 1969]; [Arnett 1985]	1026.
Cryptochaetidae			
*Cryptochaetum tuberculatum** Thorpe	Thorpe 1941; [Hennig 1952]	Thorpe 1941	1027.
Braulidae			
Braula coeca Nitzsch	Imms 1942; Hassanein & Abd El-Salam 1962; Peterson 1987	Clausen 1940.	1028.
TRICHOPTERA			
Sf. Rhyacophiloidea			
Rhyacophilidae			
Agapetus fuscipes Curtis	Durand 1955; Crichton 1957	Cheesman 1986	1029.
*Rhyacophila dorsalis** (Curtis)	[Crampton 1921c]; [Evans 1921]; [Lloyd & Lloyd 1921]; [Krafka 1923]; [Peterson 1951]; [Botosaneanu 1956]; Badcock 1961; [Fotius-Jaboulet 1964]; Hickin 1968; [Wiggins 1984]	Slack 1936; Lloyd & Lloyd 1921; Wiggins 1977, 1984	1030.
Rhyacophila septentrionis (MacLachlan)	[Krafka 1923]; [Deoras 1953]; [Durand 1955]; [Crichton 1957]; Klemm 1966	[Crichton 1957]; [Gillott 1980]	1031.
Hydrobiosidae			
Hydrobiosis umbripennis MacLachlan	Tillyard 1926a	Tillyard 1926a	1032.
Glossosomatidae			
*Glossosoma** sp.	[Lloyd & Lloyd 1921]; Hickin 1968; Wiggins 1977, 1984]	Hickin 1968; Wiggins 1977, 1984	1033.

taxon	mouthpart-morphology data	dietary data	no.
Hydroptilidae			
Agraylea multipunctata Curtis	[Durand 1955]; Crichton 1957; [Wiggins 1984]	[Crichton 1957]; [Gillott 1980]	1034.
*Hydroptila** sp.	Das 1938; Hickin 1968; Wiggins 1977; Morse & Holzenthal 1984	Wiggins 1977, 1984	1035.
Sf. Hydropsychoidea			
Philopotamidae			
Dolophiloides distinctus (Walker)	Crampton 1920b; [Wiggins 1984]	[Crichton 1957]; [Gillott 1980]	1036.
*Dolophiloides distinctus** (Walker)	[Das 1938]; [Badcock 1961]; Wallace & Malas 1976; [Wiggins 1977, 1984]; [Cowley 1978]	Wallace & Malas 1976; Wiggins 1984	1037.
*Wormaldia occipitalis** (Pictet)	[Boftosaneanu 1956]; Satija & Satija 1959; Hickin 1968; Wiggins 1984	Satija & Satija 1959; Wiggins 1984	1038.
Stenopsychidae			
Pseudostenopsyche sugens Döhler	Döhler 1915; Crichton 1957	[Crichton 1957]; [Gillott 1980]	1039.
Hydropsychidae			
Hydropsyche angustipennis (Curtis)	[Genthe 1898]; [Deoras 1943]; [Durand 1955]; Crichton 1957	[Deoras 1944]; [Gillott 1980]	1040.
*Hydropsyche fulvipes** (Curtis)	[Krafka 1923]; Sattler 1958; [Das 1938]; [Badcock 1961]; [Wiggins 1977, 1984]; Morse & Holzenthal 1984]	Slack 1936; Wiggins 1977, 1984	1041.
*Macronema zebratum** Hagen	Peterson 1951; Wiggins 1977; 1978; [Morse & Holzenthal 1984]	Peterson 1951; Wiggins 1977, 1984	1042.
Polycentropodidae			
*Plectrocnemia conspersa** (Curtis)	Hickin 1968; [Cowley 1978]	Hickin 1968; [Wiggins 1984]	1043.
Polycentropus flavomaculatus (Pictet)	Deoras 1943; Crichton 1957; [Wiggins 1984]	[Deoras 1944]; [Gillott 1980]	1044.
Dipseudopsidae			
Dipseudopsis africana Ulmer	Ulmer 1905; [Cummings 1913]; [Crampton 1923b]; [Crichton 1957]	[Crichton 1957]; [Gillott 1980]	1045.
Ecnomidae			
Ecnomus tenellus (Rambur)	Durand 1955; Crichton 1957	Chessman 1986	1046.
Psychomyiidae			
Tinodes waeneri (Linneaus)	Durand 1955; Crichton 1957	[Crichton 1957]; [Gillott 1980]	1047.
Xiphocentronidae			

taxon	mouthpart-morphology data	dietary data	no.
Sf. Limnephiloidea			
Phryganeidae			
*Philostomis postica** (Walker)	Lloyd & Lloyd 1921; Krafka 1923; [Das 1938]; [Wiggins 1977, 1984]	Wiggins 1977, 1984	1048.
*Phryganea cinera** Walker	[Lloyd & Lloyd 1921]; Wiggins 1960, 1977; [Badcock 1961]; [Hinton 1963]; [Hickin 1968]	[Lloyd & Lloyd 1921]; Milne & Milne 1981; Wiggins 1984	1049.
Phryganea striata Linneaus	[Cummings 1914b]; [Durand 1955]; Crichton 1957	Crichton 1957	1050.
Phryganopsychidae			
*Phryganopsyche latipennis** (Banks)	Wiggins 1959	Wiggins 1959	1051.
Brachycentridae			
Brachycentrus subnubilus Curtis	Crichton 1957; [Wiggins 1984]	Crichton 1957	1052.
Limnecentropodidae			
Chathamiidae			
*Philansus plebius** (Walker)	Anderson & Lawson-Kerr 1976; Leader 1976; Cowley 1978	Leader 1976; Anderson, Fletcher & Lawson-Kerr 1977	1053.
Tasimiidae			
Tasimia natasia Mosely	Mosely 1936; Riek 1968b; Neboiss 1977	Riek 1968b; [Wiggins 1982]	1054.
Limnephilidae			
Anabolia furcata Leach	Lucas 1893; Kellogg 1895; [Ulmer 1905; [Deoras 1943]	[Deoras 1944]; Gillott 1980]	1055.
*Anabolia furcata** Leach	Lucas 1893; [Krafka 1923]; Wiggins 1977, 1984	Wiggins 1977, 1984	1056.
*Drusus trifidus** MacLachlan	[Botosaneanu 1956]; Fotius-Jaboulet 1961; [Hickin 1968]	Wiggins 1977, 1984	1057.
*Dicosmoecus** sp.	Peterson 1951; Wiggins 1977	Peterson 1951	1058.
*Limnephilus flavicornis** Fabricius	[Krafka 1923]; Winkler 1959; [Barbier 1961]; [Hickin 1968]; [Wiggins 1977]	Hickin 1968; Wiggins 1977, 1984	1059.
Limnephilus lunatus Curtis	[Packard 1898]; [Durand 1955]; Crichton 1957; [Richards & Davies 1977]; Wiggins 1984	[Critchon 1957]; [Gillott 1980]	1060.
*Stenophylax permistus** MacLachlan	Frochot 1962; [Hickin 1968]	Slack 1936; [Wiggins 1984]	1061.
Goeridae			
Goera pilosa Fabricius	[Deoras 1943]; Durand 1955; Crichton 1957	[Crichton 1957]; [Gillott 1980]	1062.
*Goera pilosa** Fabricius	[Lloyd & Lloyd 1921]; Krafka 1923; Hickin 1968; [Wiggins 1977]	Hickin 1968; Wiggins 1984	1063.

taxon	mouthpart-morphology data	dietary data	no.
Thremmatidae			
*Thremma anomalum** MacLachlan	Botosaneanu 1956; Giudicelli 1971	Botosaneanu 1956; Giudicelli 1971	1064.
Uenoidae			
Lepidostomatidae			
*Lepidostoma hirtum** (Fabricius)	[Krafka 1923]; Hickin 1968; [Wiggins 1977]	Hickin 1968; Wiggins 1977, 1984	1065.
Oeconesidae			
Zelandopsyche ingens Tillyard	Tillyard 1921; Cowley 1978	[Wiggins 1982]	1066.
Kokiriidae			
Taskiropsyche lacustris Neboiss	Neboiss 1977	[Wiggins 1982]	1067.
Plectrotarsidae			
Plectrotarsus gravenhorstii Kolenati	Ulmer 1905; Cummings 1914a; Crampton 1923b; Mosely 1936; Crichton 1957	[Gillott 1980]	1068.
Beraeidae			
Beraea maurus Curtis	Crichton 1957; [Wiggins 1984]	[Crichton 1957]; [Gillott 1980]	1069.
Sericosomatidae			
Crunoecia irrorata (Curtis)	Crichton 1957	[Crichton 1957]; [Gillott 1980]	1070.
Notidobia ciliaris (Linneaus)	Cummings 1914b; Durand 1955; Crichton 1957	[Crichton 1957]; [Gillott 1980]	1071.
*Notidobia cilaris** (Linneaus)	Hickin 1968	Hickin 1968	1072.
Sericostoma personatum (Spence)	Cummings 1914b; Crichton 1957	[Crichton 1957]; [Gillott 1980]	1073.
Conoesucidae			
*Pycnocentria sylvestris** McFarlane	Cowley 1978	Cowley 1978	1074.
Antipodoeciidae			
Calocidae			
Tamasia variegata Mosely	Mosely 1936; Neboiss 1977	Mosely 1936; [Wiggins 1982]	1075.
Helicophidae			
*Zelolessica cheira** McFarlane	Cowley 1978	Cowley 1978	1076.
Molannidae			
Molanna angustata Curtis	Crichton 1957; [Wiggins 1984]	[Crichton 1957]; [Gillott 1980]	1077.
*Molanna angustata** Curtis	[Krafka 1923]; Badcock 1961; Hinton 1963; Hickin 1968; [Wiggins 1977, 1984]	Wiggins 1984	1078.
Odontoceridae			
Odontocerum albicorne (Scopoli)	Crichton 1957	[Crichton 1957]; Gillott 1980	1079.
*Odontocerum albicorne** (Scopoli)	Hinton 1963; Hickin 1968;	Lloyd & Lloyd 1921	1080.

taxon	mouthpart-morphology data	dietary data	no.
_Psilotreta_* sp.	Lloyd & Lloyd 1921; Crampton 1921c; Krafka 1923; Morse & Holzenthal 1984; Wiggins 1977, 1984	Wiggins 1984	1081.
Atriplectididae			
_Atriplectides dubius_* Mosely	Neboiss 1978	diet undocumented	1082.
Philorheithridae			
Tasmanthrus angustipennis Mosely	Mosely 1936; Neboiss 1977	Mosely 1936; [Wiggins 1982]	1083.
Helicopsychidae			
_Helicopsyche borealis_* (Hagen)	Lloyd & Lloyd 1921; Krafka 1923; Wiggins 1977, 1984	Wiggins 1977, 1984	1084.
Calamoceratidae			
_Heteroplectron americanum_* Walker	Lloyd & Lloyd 1921; Krafka 1923; Wiggins 1977	Wiggins 1977, 1984	1085.
Leptoceridae			
Athripsodes cinera Curtis	Crichton 1957	Crichton 1957	1086.
Mystacides sepulchralis Walker	Kellogg 1895; [Deoras 1943]	[Deoras 1944]; Crichton 1957	1087.
LEPIDOPTERA			
So. Zeugloptera			
Sf. Micropterygoidea			
Heterobathmiidae			
Heterobathmia pseuderiacrania Philpott	Kristensen & Nielsen 1979	Kristensen 1984b	1088.
_Heterobathmia pseuderiacrania_* Philpott	Kristensen & Nielsen 1979, 1983	Hudson 1928; Kristensen & Nielsen 1983; Kristensen 1984b	1089.
Micropterygidae			
Micropteryx calthella Linneaus	Walter 1885; [Packard 1895]; [Busck & Böving 1914]; [Crampton 1923b]; Philpott 1927; Pirngruber 1944; Portier 1949; Hannemann 1956; Kristensen & Nielsen 1979; Chauvin & Faucheux 1981	Heath 1959; Kristensen 1984b	1090.
_Micropteryx calthella_* Linneaus	Packard 1895; [Busck & Böving 1914]; Portier 1949; Lorenz 1961	Peterson 1948; Dumbleton 1952; Carter & Dugdale 1982; Kristense 1984b	1091.
Mnemonica auricyanea Walsingham	Busck & Böving 1914; Crampton 1920b; Philpott 1927; Snodgrass 1928, 1935; [Ferris 1943]; Portier 1949	Kristensen 1984b	1092.
Palaeomicroides fasciatella Issiki	Issiki 1931	Kristensen 1984b	1093.
Sabatinca auruncella Hudson	Genthe 1898; Tillyard 1923; Philpott 1927; [Issiki 1931]; Portier 1949; Snodgrass 1961	Kristensen 1984b; Thien et _al._ 1985	1094.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
*Sabatinca barbarica** Philpott	Tillyard 1922; [Snodgrass 1935]	Hudson 1928, 1939; Schutze 1931; Ford 1949; Yasuda 1962; Kristensen 1984b	1095.
So. **Dacnonypha**			
Sf. **Agathiphagoidea**			
Agathiphagidae			
Agathiphaga vitiensis Dumbleton	Dumbleton 1952; Kristensen 1984b	diet undocumented	1096.
*Agathiphaga vitiensis** Dumbleton	Dumbleton 1952; Kristensen 1984a	Dumbleton 1952; Common 1973; Kristensen 1984b	1097.
Sf. **Eriocranoidea**			
Eriocraniidae			
*Eriocrania sangi** Wood	[Tragardh 1913]; Jayewickreme 1940; [Hasenfuss 1969]	Jayewickreme 1940	1098.
Eriocrania semipurpurella Stephens	Tillyard 1923; Philpott 1927; [Portier 1949]; Snodgrass 1961; Kristensen 1968a	Kristensen 1984b	1099.
Lophocoronidae			
Lophocorona pediasia Common	Common 1973	Common 1973	1100.
Acanthopteroctetidae			
Sf. **Neopseustoidea**			
Neopseustidae			
Archepiolus schmidi Mutuura	Mutuura 1971	[Kristensen 1968c]	1101.
Neopseustis meyricki Hering	Kristensen 1968c	[Kristensen 1968c]	1102.
So. **Exoporia**			
Sf. **Mnesarchaeoidea**			
Mnesarchidae			
Mnesarchea loxoscia Meyrick	Tillyard 1923; Philpott 1927; [Kristensen 1968c, 1979]; Kristensen & Nielsen 1981	Kristensen & Nielsen 1981	1103.
Sf. **Hepialoidea**			
Prototheoridae			
Neotheoridae			
Neotheora chiloides Kristensen	Kristensen 1978	Kristensen 1978	1104.
Anomosetidae			
Palaeosetidae			
Palaeophatidae			
Azaleodes fuscipes Nielsen	Nielsen 1987	diet undocumented	1105.
Hepialidae			
Afrotheora thermodes (Meyrick)	Nielson & Scoble 1986	Nielson & Scoble 1986	1106.
Hepialus sp.	Kellogg 1895; Philpott 1927	Richards & Davies 1977	1107.
*Hepialus humuli** Linneaus	[Forbes 1910]; [Crampton 1921c]; Hinton 1947; Hasenfuss 1969	Forbes 1923; Meikle 1937; Pinhey 1975; [Ottosson & Anderson 1983]	1108.
Stenopis thule Strecker	Mosher 1915	Richards & Davies 1977	1109.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
So. Monotrysia			
Sf. Nepticuloidea			
Nepticulidae			
_Ectoedemia heinrichi_* Busck	DeGryse 1915; [Heinreich 1918]; [MacKay 1972]	[Peterson 1948]; [Arnett 1985]	1110.
_Nepticula malella_* Stainton	[Tragardh 1913]; [Heinreich 1918]; [Jayewickreme 1940]; Briolini 1960; [MacKay 1972]	Jayewickreme 1940; MacKay 1972	1111.
Opostegidae			
_Opostega_* sp.	Heinreich 1918	[Arnett 1985]	1112.
Tischeriidae			
_Tischeria marginea_* Haworth	[Tragardh 1913]; Heinreich 1918; Jayewickreme 1940; Hasenfuss 1969	Jayewickreme 1940; [Arnett 1985]	1113.
Sf. Incurvarioidea			
Incurvariidae			
_Paraclemensia acerifoliella_* Fitch	Peterson 1948; MacKay 1972	MacKay 1972; Arnett 1985	1114.
Tegeticula yuccasella (Riley)	Packard 1898; Berlese 1909; Crampton 1923b; [Philpott 1927]; Portier 1949	Powell & Mackie 1966; Davis 1967; Baker 1986	1115.
_Prodoxus quinquepunctella_* Chambers	Peterson 1948; MacKay 1972	Peterson 1948; Arnett 1985	1116.
Heliozelidae			
_Coptodisca splendoriferella_* Clemens	Snodgrass 1922b; Peterson 1948	Peterson 1948; Arnett 1985	1117.
So. Ditrysia			
Sf. Tineoidea			
Tineidae			
_Lindera tessellatella_* Zeller	Hinton 1957	Hinton 1957	1118.
_Tinea pellionella_* (Linneaus)	Hinton [1943], 1957; Peterson 1948; [Portier 1949]; Werner 1958	Peterson 1948; Hinton 1957; Arnett 1985	1119.
Acrolophidae			
Psychidae			
_Thrydopteryx ephemeraeformis_* Haworth	Ripley 1923; Snodgrass 1928; Peterson 1948; Grimes & Neunzig 1986a	Arnett 1985	1120.
Pseudarbelidae			
Eriocottidae			
Eriocottis fuscanella Zeller	Nielsen 1978	Nielsen 1978	1121.
Arhennophanidae			
Ochsenheimeriidae			
Ochsenheimeria vacculella Roessler-Stamm	Davis 1975	diet undocumented	1122.
Phyllocnistidae			
_Phyllocnistis suffusella_* Zeller	[Tragardh 1913]; Jayewickreme 1940; Grandi 1959	Jayewickreme 1940; Powell 1980	1123.
Gracillariidae			
_Gracillaria stigmatella_* Fabricius	[Tragardh 1913]; [DeGryse 1915]; Grandi 1915, 1959; [MacKay 1972]	Hering 1954; Powell 1980	1124.

taxon	mouthpart-morphology data	dietary data	no.
Lyonetiidae			
*Bdellia somnulentella** Zeller	Jayewickreme 1940; MacKay 1972	MacKay 1972; Arnett 1985	1125.
*Paraleucoptera sinuella** Reutti	Briolini 1965	Briolini 1965	1126.
Sf. Gelechioidea			
Oecophoridae			
*Depressaria heracliana** DeGeer	[Forbes 1910]; Peterson 1948; MacKay 1972	Clarke 1941; MacKay 1972	1127.
Oecophora bractella (Linneaus)	[Philpott 1927]; Clarke 1941	[Richards & Davies 1977]	1128.
Ethmiidae			
*Ethmia longimaculella** Chambers	[Peterson 1948]; MacKay 1972	MacKay 1972	1129.
Stenomatidae			
Eriogenes mesogypsa Meyrick	Duckworth 1973	[Richards & Davies 1977]	1130.
*Stenoma schlaegeri** Zeller	McKay 1972	McKay 1972	1131.
Xyloryctidae			
Stathmopodidae			
Pterolonchiidae			
Coleophoridae			
*Coleophora veroniella** Chambers	DeGryse 1915; [Peterson 1948]	[Arnett 1985]; [Davidson & Lyon 1987]	1132.
Blastobasidae			
*Valentinia glanduella** (Riley)	MacKay 1972	MacKay 1972; Arnett 1985	1133.
Symmocidae			
Elachistidae			
Elachista madarella (Clemens)	[Genthe 1898]; [Philpott 1927]; Braun 1948.	Braun 1948	1134.
Coelopoetidae			
Batracheidae			
Momphidae			
*Ithome concolorella** (Chambers)	Zimmerman 1978	Balduf 1974	1135.
Blastodacnidae			
Gelechiidae			
*Aristotlea hermanella** (Fabricius)	Jayewickreme 1940; MacKay 1972	MacKay 1972	1136.
*Gnorimoschema gallaesolidagnis** Riley	[Peterson 1948]; MacKay 1972	MacKay 1972	1137.
Scythrididae			
*Scythris epilobiella** McDunnough	MacKay 1972	MacKay 1972	1138.
Agonoxenidae			
Cosmopterygidae			
Cosmopteryx zieglerella Huebner	[Philpott 1927]; Hodges 1962	Hodges 1962; Powell 1980	1139.
Sf. Alucitoidea			
Copromorphidae			
Carposinidae			
*Carposina fernaldana** Busck	MacKay 1972	MacKay 1972; Arnett 1985	1140.
Alucitidae			
Epermeniidae			
*Epimerina albapunctella** Busck	MacKay 1972	MacKay 1972	1141.

taxon	mouthpart-morphology data	dietary data	no.
Glyphipterigidae			
*Anthophila pariana** Clerck	MacKay 1972	MacKay 1972; Arnett 1985	1142.
Sf. Yponomeutoidea			
Yponomeutidae			
*Attera aurea** Fitch	Peterson 1948; MacKay 1972	MacKay 1972; Powell 1980; [Arnett 1985]	1143.
Amphitheridae			
Argyesthiidae			
Douglasiidae			
Acrolepiidae			
Heliodinidae			
Schreckensteiniidae			
Sf. Sesioidea			
Choreutidae			
Sesiidae			
Sanninoidea sp.	Snodgrass 1935; Borror, DeLong & Triplehorn 1976	[Arnett 1985]	1144.
*Podosesia syringae** (Harris)	Peterson 1948	Peterson 1948	1145.
Sf. Immoidea			
Immidae			
Imma sp.	Meyrick 1906; Philpott 1927; Holloway *et al.* 1987	[Common 1979]; Holloway *et al.* 1987	1146.
Sf. Cossoidea			
Cossidae			
*Cossus cossus** Linneaus	Forbes 1910; Strenger 1952; Werner 1958	Uvarov 1928; Powell 1980	1147.
*Prionoxystus robiniae** (Peck)	[Crampton 1921c]; Snodgrass 1928; 1928; Peterson 1948; MacKay 1972; [Grimes & Neunzig 1986]	Uvarov 1928; Powell 1980	1148.
*Zeuzera pyrina** Linneaus	Ripley 1923; Peterson 1948	Peterson 1948; Arnett 1985	1149.
Metarbelidae			
Dudgeoneidae			
Sf. Tortricoidea			
Tortricidae			
*Archips cerasivorana** (Fitch)	Forbes 1910; Peterson 1948; [Grimes & Neunzig 1986b]	Peterson 1948; Arnett 1985	1150.
*Choristoneura argyrospila** (Walker)	Peterson 1948; [Grimes & Neunzig 1986a, 1986b]	Powell 1980; [Arnett 1985]	1151.
Choristoneura fumiferana (Clemens)	Mosher 1915; Freeman 1947	Milne & Milne 1980	1152.
*Cydia pomonella** Linneaus	Bordas 1909; Lopez 1932; Peterson 1948; Bradley, Tremewan & Smith 1973	Powell 1980; [Hill 1983]; Arnett 1985	1153.
Cochylidae			
Stenodes alternana (Stephens)	Bradley, Tremewan & Smith 1983	Bradley, Tremewan & Smith	1154.

taxon	mouthpart-morphology data	dietary data	no.
Sf. Zygaenoidea			
Heterogynidae			
Zygaenidae			
*Harrisina americana** Guernee	Peterson 1948	Peterson 1948; Arnett 1985	1155.
Chrysopolomidae			
Somatobrachyidae			
Somatobrachys infuscata Klug	Jordan 1916	diet undocumented	1156.
Megalopygidae			
*Lagoa crispata** (Packard)	Forbes 1910; [Peterson 1948]	Arnett 1985	1157.
Limacodidae			
Dalceridae			
Epipyropidae			
Epipomponia elongata Jordan	Jordan 1928	diet undocumented	1158.
Cyclotornidae			
Sf. Castnioidea			
Castniidae			
Castnia icarus	Miller 1971	[Scott 1986]	1159.
Sf. Hesperoidea			
Hesperiidae			
Epargyreus clarus Cramer	Ehrlich 1960; [Schmitt 1938]	Scott 1986	1160.
Panoquina ocola Edwards	Ehrlich & Ehrlich 1962	Scott 1986	1161.
Quinta cannae (Herrich-Schaffer)	Miller 1971	Scott 1986	1162.
Tagiades flesus (Fabricius)	Miller 1971	diet undocumented	1163.
Urbanus dorantes (Stoll)	Miller 1971	Pyle 1981; Scott 1986	1164.
Megathymidae			
Megathymus yuccae (Boisduval & LeConte)	Miller 1971	Scott 1986	1165.
Sf. Papilionoidea			
Papilionidae			
Battus philenor Linneaus	Ehrlich & Ehrlich 1962	Pyle 1981; Scott 1986	1166.
Papilio demoleus Linneaus	[Schmitt 1938]; Vasudeva 1956; Srivastava 1957; [Ehrlich 1958b]; [Ehrlich & Ehrlich 1962]	[Arnett & Jacques 1981]; [Pyle 1981]; DeVries 1983	1167.
Parides iphidamus Fabricius	Ehrlich & Ehrlich 1962	[Scott 1986]	1168.
Teinopalpus imperalis Hope	Ehrlich 1958b	[Arnett 1985]	1169.
Pieridae			
Eurema deva Doubleday	Ehrlich & Ehrlich 1962	[Arnett & Jacques 1981]; [Scott 1986]	1170.
Pieris brassicae Linneaus	[Breitenbach 1882]; [Schmitt 1938]; Portier 1949; Eastham & Eassa 1955; [Ehrlich & Ehrlich 1962]; Eassa 1963a, 1963b	Nenjukov 1927; Uvarov 1928; [Hill 1983]; Scott 1986	1171.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
Lycaenidae			
Celastrina argiolus Linneaus	Ehrlich & Ehrlich 1962	Scott 1986	1172.
Lycaena helloides Boisduval	[Taylor 1957]; Ehrlich 1958b	[Arnett & Jacques 1981]; Scott 1986	1173.
Riodinidae			
Apodemia palmeri Edwards	Ehrlich & Ehrlich 1962	Scott 1986	1174.
Lasaia agesilas Latreille	Ehrlich & Ehrlich 1962	Scott 1986	1175.
Libytheidae			
Ithomiidae			
Danaidae			
Danaus archippus (Fabricius)	Burgess 1880; Kellogg 1893, 1895; [Schmitt 1938]; DuPorte 1956, 1957; [Taylor 1957]; [Ehrlich 1958a]; [Ehrlich & Davidson 1961]; [Ehrlich & Ehrlich 1962]; [Evans 1984]	[Arnett & Jacques 1981]; Arnett 1985; Scott 1986	1176.
Satyridae			
Brassolidae			
Morphidae			
Amalthusiidae			
Nymphalidae			
Anartia fatima Fabricius	Ehrlich & Ehrlich 1962	Scott 1986	1177.
*Basilarcha archippus** Cramer	[Forbes 1910]; Peterson 1948	Peterson 1948; Scott 1986	1178.
Calinaga budda Moore	Ehrlich 1958b	diet undocumented	1179.
Heliconius charitonia Linneaus	Ehrlich & Ehrlich 1962	Arnett & Jacques 1981; Scott 1986	1180.
Vanessa cardui Linneaus	[Kirbach 1883, 1884]; [Walter 1885]; Ehrlich & Ehrlich 1962	Arnett & Jacques 1981; Scott 1986	1181.
*Vanessa cardui** Linneaus	[Bordas 1909]; Grimes & Neunzig 1986a, 1986b	Arnett & Jacques 1981; Scott 1986	1182.
Acraeidae			
Sf. Pterophoroidea			
Pterophoridae			
*Platyptilia carduidactyla** Riley	Peterson 1948; Grimes & Neunzig 1986a, 1986b	Peterson 1948; [Arnett 1985]	1183.
Tineodidae			
Oxychirotidae			
Sf. Pyraloidea			
Thyrididae			
Neobansia fuliginea Whalley	Whalley 1971	Whalley 1971	1184.
Hyblaeidae			

taxon	mouthpart-morphology data	dietary data	no.
Pyralidae			
*Acroia grisella** (Fabricius)	Crampton 1921c; Hinton 1943; Peterson 1948	Peterson 1948; Arnett 1985	1185.
Bissetia steniellus	Puri 1958	[Richards & Davies 1977]	1186.
Chilo tumidicostalis Hampson	[Genthe 1898]; Puri 1957, [1958]	Puri 1957	1187.
Chilotraea infuscatellus	Puri 1958	diet undocumented	1188.
*Galleria mellonella** Linneaus	Das 1938; [Ferris 1943]; Hinton 1943; Peterson 1948; Grimes & Neunzig 1986b	Wollman 1911; Uvarov 1928; Arnett 1985	1189.
Haritala ruralis (Scopoli)	Rouchy 1964	diet undocumented	1190.
*Homoeosoma electellum** (Hulst)	Grimes & Neunzig 1986b	Arnett 1985; Davidson & Lyon 1987	1191.
Scirpophaga nivella (Fabricius)	[Philpott 1927]; Pradhan & Aren 1941; Puri 1958	[Richards & Davies 1977]	1192.
Sf. Drepanoidea			
Thyatiridae			
*Euthyatira** sp.	Peterson 1948	Peterson 1948	1193.
Drepanidae			
*Drepana arculata** Walker	Forbes 1910	Arnett 1985	1194.
Sf. Geometroidea			
Geometridae			
*Ourapteryx sambucaria** Linneaus	Short 1951	[Arnett 1985]	1195.
Apoprogonidae			
Epiplemidae			
Sematuridae			
Axiidae			
Uraniidae			
Epicopeiidae			
Sf. Calliduloidea			
Callidulidae			
Pterothysanidae			
Sf. Mimallonoidea			
Mimallonidae			
*Lacosoma chiridota** Grote	Forbes 1910	Peterson 1948; Arnett 1985	1196.
Sf. Bombycoidea			
Apatelodidae			
Bombycidae			
*Bombyx mori** (Linneaus)	Grandi 1924a; Peterson 1948; Snodgrass 1961; Richards & Davies 1977	Peterson 1948; Arnett 1985	1197.
Eupterotidae			
Anthelidae			
Brahmaeidae			

taxon	mouthpart-morphology data	dietary data	no.
Lasiocampidae			
_Malacosoma americana_* (Fabricius)	[Forbes 1910]; Snodgrass 1928; 1947, 1960, 1961; Peterson 1948; Grimes & Neunzig 1986b	Arnett & Jacques 1981; Arnett 1985	1198.
Malacosoma neustria Linneaus	[Schmitt 1938]; [Snodgrass 1961]; Rouchy 1964	[Snodgrass 1961]	1199.
Endromidae			
Lemoniidae			
Ratardidae			
Carthaeidae			
Carthaea saturnoides Walker	Common 1966	Common 1966	1200.
Oxytenidae			
Cercophanidae			
Saturniidae			
_Automeris io_* (Fabricius)	Forbes 1910; Peterson 1948	Peterson 1948; Milne & Milne 1980; Arnett 1985	1201.
Dryocampa rubicunda (Fabricius)	Mosher 1915	Milne & Milne 1980	1202.
Eacles imperalis (Drury)	Michener 1952	Milne & Milne 1980	1203.
_Telea polyphemus_* Cramer	Forbes 1910; Peterson 1948	Arnett 1985	1204.
Sf. Sphingoidea			
Sphingidae			
_Acherontia atropos_* Linneaus	Bordas 1909; Portier 1949	Portier 1949	1205.
Agrius convolvuli (Linneaus)	Berlese 1909; Snodgrass 1935; Portier 1949; Richards & Davies 1977	Arnett 1985	1206.
Dilina tiliae (Linneaus)	[Philpott 1957]; Short 1951	diet undocumented	1207.
_Dilina tiliae_* (Linneaus)	Short 1951	diet undocumented	1208.
_Dolba hyloeus_* (Drury)	Forbes 1910	Peterson 1948; Arnett 1985	1209.
Manduca sexta (Linneaus)	Berlese 1909; Portier 1949	[Milne & Milne 1980]	1210.
_Manduca sexta_* (Linneaus)	Peterson 1912, 1948; [Dethier 1937]; [DuPorte 1956]	Arnett 1985	1211.
Sf. Noctuoidea			
Dioptidae			
Thyretidae			
Notodontidae			
_Schizura concinna_* (Smith)	Forbes 1910; Crampton 1921c; Peterson 1948; [Grimes & Neunzig 1986a, 1986b]	Milne & Milne 1980; Arnett 1985	1212.
Thaumetopoeidae			

taxon	mouthpart-morphology data	dietary data	no.
Lymantriidae			
*Orgyia leucostigma** (Smith)	Kellogg 1902; Snodgrass 1947; Peterson 1948	Milne & Milne 1980; Arnett 1985	1213.
Arctiidae			
*Estigmene acrea** (Drury)	Snodgrass 1928, 1935	Milne & Milne 1980	1214.
*Euchaetes egle** (Drury)	Forbes 1910	Peterson 1948; Arnett 1985	1215.
Hyphantria cunea (Cunea)	Snodgrass 1935; Borror, DeLong & Triplehorn 1976	Milne & Milne 1980	1216.
*Pyrrharctia isabella** (Smith & Abbott)	Dethier 1937; Peterson 1948	Arnett 1985	1217.
Lithosiidae			
Ctenuchidae			
Ctenuchia sp.	Crampton 1923b; [Richards & Davies 1977]	[Milne & Milne 1980]; Arnett 1985	1218.
Pericopidae			
Hypsidae			
Nolidae			
Noctuidae			
Calyptra eustrigata (Hampson)	Banziger 1970, 1971, [1980]; Smith 1985	Banziger 1970; Cochereau 1974	1219.
Catocala sp.	Kellogg 1893, 1895; Schmitt 1938	[Milne & Milne 1980]	1220.
*Catocala** sp.	Forbes 1910; Peterson 1948; [Crumb 1956]	Peterson 1948; Arnett 1985	1221.
*Lacinipolia renigera** (Stephan)	Ripley 1923; [Hinton 1947]; [Crumb 1956]	Peterson 1948; Arnett 1985	1222.
Othreis materna (Linneaus)	[Darwin 1875]; Srivastava & Bogawat 1969; Banziger 1982	Srivastava & Bogawat 1969; [Banziger 1982]	1223.
*Papaipema nitela** Guenee	DeGryse 1915; [Peterson 1948]	[Arnett 1985]	1224.
*Peridroma magaritosa** (Haworth)	Ripley 1923; Snodgrass 1928; [Crumb 1956]	Arnett 1985	1225.
*Pseudaletia unipuncta** (Haworth)	Ripley 1923; Peterson 1948	Peterson 1948; Arnett 1985	1226.
*Spodoptera eridania** (Cramer)	Woke 1941; Peterson 1948	Woke 1941; [Ottosson & Anderson 1983]; Arnett 1985	1227.
Agaristidae			
*Agriotis** sp.	Dyar 1896; Ripley 1923; Peterson 1948; [Crumb 1956]	[Hill 1983]; Davidson & Lyon 1987	1228.
Cocytiidae			

taxon	mouthpart-morphology data	dietary data	no.
HYMENOPTERA			
So. Symphyta			
Sf. Megalodontoidea			
Xyleidae			
Macroxyela sp.	Crampton 1921c; 1923b	[Richards & Davies 1977]	1229.
*Megaxyela** sp.	Crampton 1921c; Yuasa 1922; Peterson 1948	Peterson 1948; [Arnett 1985]	1230.
Xyela minor Norton	[Crampton 1923b]; [Berland 1947]; Snodgrass 1960	[Richards & Davies 1977]	1231.
Megalodontidae			
*Megalodontus spissicornis** Klug	Lorenz & Kraus 1957	Lorenz & Kraus 1957	1232.
Pamphiliidae			
*Neurotoma** sp.	Crampton 1921c; [Peterson 1948]; Lorenz & Kraus 1957	Arnett 1985	1233.
*Pamphilius pallipes** (Zetterstedt)	[Yuasa 1922]; Short 1952; Lorenz & Kraus 1957; [Richards & Davies 1977	Lorenz & Kraus 1957; [Comstock 1977]	1234.
Sf. Tenthredinoidea			
Cimbicidae			
*Abia americana** Cresson	Yuasa 1922; [Lorenz & Kraus 1957]	Yuasa 1922	1235.
*Cimbex americana** Leach	[Berlese 1909]; [Crampton 1921c]; Snodgrass 1935; Peterson 1948; [Lorenz & Kraus 1957]	Swan & Papp 1972; Arnett 1985	1236.
*Trichiosoma sorbi** Hartig	Lorenz & Kraus 1957; Yuasa 1922	Yuasa 1922	1237.
Tenthredinidae			
*Hoplocampa brevis** Klug	[Bird 1927]; [Peterson 1948]; [Lorenz & Kraus 1957]; Grandi 1959	[Peterson 1948]; Swan & Papp 1972	1238.
Hoplocampa halcyon Norton	Bird 1926; [Berland 1947]	[Berland 1947]; [Arnett 1985]	1239.
Macrophya pluricincta Norton	[Genthe 1898]; Matsuda 1957; [Berland 1947]	[Berland 1947]	1240.
*Pteronidea ribesii** (Scopoli)	Snodgrass 1928; Peterson 1948; Das 1938; Lorenz & Kraus 1957	Peterson 1948	1241.
Pristiphora erichsonii (Hartig)	Wong 1963; [Berland 1947]	[Berland 1947]	1242.
*Pristiphora erichsonii** Hartig)	Peterson 1948; Wong 1963; [Lorenz & Kraus 1957]	Swan & Papp 1972	1243.
Argidae			
*Arge macleayi** Leach	Peterson 1948; [Lorenz & Kraus 1957]	Peterson 1948; [Arnett 1985]	1244.

taxon	**mouthpart-morphology data**	**dietary data**	**no.**
*Dolerus similis** Norton	Yuasa 1922; Peterson 1948; [Lorenz & Kraus 1957]	Peterson 1948	1245.
Blasticotomidae			
*Blasticotoma filiceti** Klug	Enslin 1917; Lorenz & Kraus 1957	Lorenz & Kraus 1957	1246.
Pergidae			
*Acordulecera** sp.	Yuasa 1922; Peterson 1948	Yuasa 1922; Peterson 1948; [Arnett 1985]	1247.
Diprionidae			
Diprion hercyniae (Hartig)	Peterson 1948; [Arora 1953]	Peterson 1948	1248.
Sf. Siricoidea			
Xiphydriidae			
*Xiphydria camelus** (Linneaus)	[Yuasa 1922]; Peterson 1948; Short 1952	[Arnett 1985]	1249.
Syntexidae			
Siricidae			
*Sirex cyaneus** Fabricius	Short 1952; [Chrystal 1930]	[Swan & Papp 1972]; Milne & Milne 1980]	1250.
*Tremex columba** (Linneaus)	Yuasa 1922; Peterson 1948; Lorenz & Kraus 1957	Yuasa 1922; Arnett 1985	1251.
Orussidae			
*Orussus occidentalis** Cresson	Yuasa 1922; Rohwer 1917	Rohwer 1917; [Arnett 1985]	1252.
Sf. Cephoidea			
Cephidae			
*Janus compressus** Fabricius	[Middleton 1917]; [Yuasa 1921]; [Peterson 1948]; Grandi 1959	[Milne & Milne 1980]; [Arnett 1985]	1253.
So. Apocrita			
Div. Parasitica			
Sf. Ichneumonoidea			
Braconidae			
*Apanteles flavipes** Cameron	[Silvestri 1924]; [Short 1954]; Teotia 1964	Silvestri 1924; Milne & Milne 1980	1254.
Apanteles glomeratus (Linneaus)	Grandori 1911	Grandori 1911; Arnett 1985	1255.
Bathyaulax alami Zaka-ur-Rab	Zaka-ur-Rab 1978	[Swan & Papp 1972]	1256.
*Bracon gelechiae** Ashmead	[Glover 1934]; Naraykanan, Rao & Thakare 1955; Teotia 1964	[Swan & Papp 1972]	1257.
*Rhogas testaceus** (Spinola)	Ahmad 1943; [Chatterjee 1943]	Ahmad 1943	1258.
*Stenobracon dessae** Cameron	Alam 1952; Naryanan, Rao & Thakare 1955	Alam 1952	1259.
Aphidiidae			
Ichneumonidae			
*Eulimneria crassifemur** (Thompson)	Thompson & Parker 1930	Thompson & Parker 1930	1260.
*Pimpla nucum** Ratzeburg	Silvestri 1924; [Janvier 1933]; [Beirne 1941]; [Gerig 1960]	Silvestri 1924; [Step 1932]	1261.

taxon	mouthpart-morphology data	dietary data	no.
*Xorides** sp.	Short 1952	diet undocumented	1262.
Agriotypidae			
*Agriotypus armatus** Curtis	Short 1951	[Swan & Papp 1972]	1263.
Apozygidae			
Apozyx penyai Mason	Mason 1978	diet undocumented	1264.
Sf. Trigonaloidea			
Trigonalidae			
Pseudogonalys hahni Spinola	Bugnion 1910	Bugnion 1910	1265.
Sf. Megalyroidea			
Megalyridae			
Stephanidae			
Sf. Evanioidea			
Evaniidae			
*Evania appendigaster** (Linneaus)	Cameron 1958	Cameron 1958; Arnett 1985	1266.
Gasteruptiidae			
*Gasteruption assectator** (Linneaus)	Short 1952	Arnett & Jacques 1981; Arnett 1985	1267.
*Gasteruption jaculator** Linneaus	Crosskey 1951	[Arnett 1985]	1268.
Aulacidae			
*Aulacus striatus** Jurine	Short 1952	diet undocumented	1269.
Sf. Proctotrupoidea			
Pelecinidae			
Pelecinus sp.	Cresson 1887; DuPorte 1946	[Clausen 1940]; Milne & Milne 1980	1270.
Monomachidae			
Proctotrupidae			
*Phaenoserphus viator** Haliday	Jackson 1961	Jackson 1961	1271.
Heloridae			
*Helorus paradoxus** (Provancher)	Clancy 1946	Clancy 1946	1272.
Roproniidae			
Vanhorniidae			
Austroniidae			
Diapriidae			
Anarctopria latigaster Brues	Yoshimoto 1964	[Arnett 1985]	1273.
Scelionidae			
Platygasteridae			
*Platygaster herrickii** Packard	[Marchal 1906]; Hill & Emery 1937	Hill & Emery 1937	1274.
Sf. Ceraphronoidea			
Ceraphronidae			
*Lygocerus testaceimanus** Kieffer	Haviland 1921	Haviland 1921	1275.
Megaspilidae			
Sf. Chalcidoidea			
Chalcidae			
Comedo larvarum Linneaus	Silvestri 1924	Silvestri 1924	1276.
Monodontomerus dentipes Boheman	Bucher 1948	[Milne & Milne 1980]	1277.

taxon	mouthpart-morphology data	dietary data	no.
Leucopsidae			
Leucopsis gigas Fabricius	[Habu 1962]; Boucek 1974; Yoshimoto 1984	Boucek 1974; Arnett 1985	1278.
*Leucopsis hopei** Spinola	Janvier 1933	Janvier 1933	1279.
Eurytomidae			
*Axima zabriskiei** Howard	Burks 1966	[Brown 1982]	1280.
Torymidae			
Ceratosolen aculeatus Mayr	Grandi [1935], 1959	Barth 1985	1281.
Neosycophila omeomorpha Grandi	Grandi 1924b, 1959	Grandi 1924a; Arnett 1985	1282.
Agaonidae			
Blastophaga psenes Linneaus	Grandi [1925], 1959	Galil 1978; Janzen 1983; Arnett 1985	1283.
Pteromalidae			
*Nasonia vitripennis** Walker	Cutler 1955	[Clausen 1940]; Richards & Davies 1977	1284.
*Stenomalus liparae** (Giraud)	Short 1952	Richards & Davies 1977	1285.
Perilampidae			
*Perilampus chrysopae** Crawford	Clancy 1946	Clancy 1946; [Arnett 1985]	1286.
Perilampella raphidophorae Ferrière	Ferrière 1929	Ferrière 1929; diet unknown	1287.
Eucharitidae			
*Schizaspidia tenuicornis** Ashmead	Clausen 1923	Clausen 1923	1288.
Eupelmidae			
*Arachnophaga picea** (Howard)	Clancy 1946	Clancy 1946	1289.
Ormyridae			
Encyrtidae			
*Isodromus iceryae** Howard	Clancy 1946	Clancy 1946	1290.
Tanaostigmatidae			
Aphelinidae			
Signiphoridae			
Tetracampidae			
Elasmidae			
Myiocnema comperei Ashmead	Smith & Compere 1928	[Swan & Papp 1972]	1291.
Eulophidae			
*Pnigalio mediterraneus** Ferrière & Delucchi	Delanue & Arambourg 1967	Delanoue & Arambourg 1967	1292.
*Tetrastichus chrysopae** Crawford	Clancy 1946	Clancy 1946; [Arnett 1985]	1293.
Trichogrammatidae			
Apseudogramma popei Girault	Doutt & Viggiani 1968	[Swan & Papp 1972]	1294.
Mymaridae			
*Anagrus incarnatus** Haliday	Jackson 1961	Jackson 1961	1295.
Sf. Cynipoidea			
Ibalidae			
*Ibalia leucosporides** Hochenw	Chrystal 1930	Chrystal 1930	1296.
Liopteridae			

taxon	mouthpart-morphology data	dietary data	no.
Figitidae			
*Figites anthomyiarum** (Bouché)	James 1928	James 1928; [Arnett 1985]	1297.
Cynipidae			
*Rhodites rosae** (Linneaus)	Short 1952	[Step 1932]	1298.
Div. Aculeata			
Sf. Chrysidoidea			
Plumariidae			
Plumarius sp.	Evans 1966	Evans 1966; diet unknown	1299.
Chrysididae			
*Chrysis shanghaiensis** Smith	[Janvier 1933]; [Snodgrass 1935]; Parker 1936	Parker 1936	1300.
Dryinidae			
Tetrodontochelys ljunghii (Westwood)	Richards 1939	Richards 1939; [Swan & Papp 1972]	1301.
Eubolemidae			
Scolebythidae			
Scolebythus madecassus Evans	Evans 1963	Evans 1963	1302.
Bethylidae			
*Parasierola gallicola** Kieffer	Silvestri 1924	Silvestri 1924	1303.
Pristocera armifera (Say)	Richards 1939; Evans 1964	Evans 1964; Arnett 1985	1304.
Loboscelidiidae			
Sf. Tiphioidea			
Tiphiidae			
*Elaphroptera erythrura** Spinola	Janvier 1933	Janvier 1933	1305.
Sapygidae			
Fedtsckhenkia grossa De Saussure	De Saussure 1880; Brothers 1975	De Saussure 1880	1306.
Mutillidae			
*Mutilla lunulata**	Janvier 1933	Janvier 1933	1307.
Sierolomorphidae			
Bradynobaenidae			
Bradynobaenus sp.	Brothers 1975	diet undocumented	1308.
Sf. Pompiloidea			
Rhopalosomatidae			
*Rhopalosoma** sp.	Gurney 1953	Gurney 1953	1309.
Pompilidae			
*Dipogon sayi** Banks	Evans 1959	Evans 1959	1310.
*Pepsis thisbe** Lucas	Evans 1959	Evans 1959	1311.
*Pseudagenia carbonaria** Scopoli	Grandi 1926	Grandi 1926	1312.
Sf. Formicoidea			
Formicidae			
*Aphaenogaster subterranea** Latreille	[Peterson 1948]; Picquet 1958; [Kusnezov 1954b]	Milne & Milne 1980	1313.
Atta sexdens Linneaus	[Wheeler 1927]; Bugnion 1930; Kusnezov 1954a	Wilson 1971; [Hill 1983]; Arnett 1985	1314.

taxon	mouthpart-morphology data	dietary data	no.
Camponotus ligniperda Latreille	[Wheeler 1927]; Bugnion 1927, 1930; [Osten 1982]	[Arnett & Jacques 1981]	1315.
*Camponotus vagus** Scopoli	[Wheeler 1927]; Bugnion 1927, 1930; [Wilson 1975]; [Osten 1982]	[Milne & Milne 1980]; [Arnett & Jacques 1981]	1316.
Cataglyphis bicolor Fabricius	Bugnion 1930	Wilson 1971	1317.
Dolichoderis garbei Forel	[Wheeler 1927]; Bugnion 1930	[Richards & Davies 1977]	1318.
Dorylus wilverthi (Emery)	Bugnion 1930; Gotwald 1969	Wilson 1971	1319.
Ection burchelli Westwood	Wheeler 1927; Gotwald 1969	Wilson 1971	1320.
*Formica rufa** Linneaus	[Wheeler 1927]; Picquet 1958; [Kusnezov 1954b]	Wilson 1971	1321.
Messor structor Latreille	Bugnion 1930; [Kusnezov 1954b]	Uvarov 1928; Wilson 1971	1322.
Oecophylla smaragdina Fabricius	Bugnion 1927, 1930; [Gotwald 1973]	Hill 1983	1323.
Paltothyreus tarsatus Fabricius	Bugnion 1930	Wilson 1971	1324.
Sf. Scolioidea			
Scoliidae			
Scolia bidens	Bugnion 1919; [Osten 1982]; [Plant & Paulus 1987]	[Milne & Milne 1980]	1325.
Sf. Vespoidea			
Masaridae			
Paragia odyneroides Smith	Richards 1962	[Richards 1962]	1326.
Eumenidae			
*Eumenes unguiculus** Villers	Grandi 1959; [Richards 1962]	Milne & Milne 1980; [Arnett 1985]	1327.
Vespidae			
*Polistes galliacus** (Linneaus)	Parker 1943; [Snodgrass 1947]; [Grandi 1959]	[Arnett & Jacques 1981]; West-Eberhard 1983	1328.
Polistes olivaceous (DeGeer)	[Smith 1898]; [Grandi 1959]; Seghal 1963	Milne & Milne 1980; [Arnett & Jacques 1981]	1329.
Vespa vulgaris Linneaus	Berlese 1909; Kirmayer 1909; [Liu 1925]; [Snodgrass 1928, 1960]; Strenger 1952; [Nedel 1960]; Richards 1962; [Richards & Davies 1977]	[Milne & Milne 1980]; Hill 1983	1330.
Vespula germanica (Fabricius)	[Snodgrass 1944]; [Ross 1965]; Richards & Davies 1977	Milne & Milne 1980; Hill 1983	1331.

taxon	mouthpart-morphology data	dietary data	no.
*Vespula sylvestris** (Scopoli)	Short 1952	Milne & Milne 1980; [Hill 1983]	1332.
Sf. Sphecoidea			
Sphecidae			
*Ammophila campestris** Latreille	[Kellogg 1902]; Grandi 1926; [Bohart & Mencke 1976]	Grandi 1926; [Arnett 1985]	1333.
Ammophila subulosa (Linneaus)	[Kellogg 1902]; Ulrich 1924; [Osten 1982]	[Arnett & Jacques 1981]	1334.
Chalybion bengalense Dahlberg	Bugnion 1929; [Bohart & Mencke 1976]	Arnett 1985	1335.
Prionyx thomae (Fabricius)	Bohart & Mencke 1976	Swan & Papp 1972	1336.
Sphex ichneumoneus (Linneaus)	Bohart & Mencke 1976	Arnett & Jacques 1981	1337.
Tachytes distinctus Smith	Williams 1913; [Bohart & Mencke 1976]	Williams 1913; [Milne & Milne 1980]	1338.
Sf. Apoidea			
Colletidae			
Colletes fulgidus Swenk	[Saunders 1891]; [DeMoll 1908]; Michener 1944; [Stephen, Bohart & Torchio 1969]; [Plant & Paulus 1987]	Arnett & Jacques 1981	1339.
Diphaglossa gayi Spinola	Janvier 1933; Stephen, Bohart & Torchio 1969	Janvier 1933	1340.
Hylaeus sp.	Saunders 1891; DeMoll 1908; Nedel 1960; Stephen, Bohart & Torchio 1969]; [Osten 1982]; [Plant & Paulus 1987]	[Arnett 1985]	1341.
Halictidae			
Halictus farinosus Smith	[Saunders 1981]; [Demoll 1908]; Michener 1944; [Stephen, Bohart & Torchio 1969]; [Osten 1982]; [Plant & Paulus 1987]	Schwartz 1948; Waage 1975	1342.
Nomia melanderi Cockerell	[DeMoll 1908]; Stephen, Bohart & Torchio 1969	Stephen, Bohart & Torchio 1969; Milne & Milne 1980	1343.
Specodes sp.	Saunders 1891; Stephen, Bohart & Torchio 1969	Arnett 1985	1344.
Andrenidae			
Andrena mimetica Cockerell	[Saunders 1891]; [Smith 1898]; [DeMoll 1908]; [Snodgrass 1935]; [Nedel 1960]; Michener 1944; [Plant & Paulus 1987]	Step 1932; [Arnett & Jacques Jacques 1981]	1345.

taxon	mouthpart-morphology data	dietary data	no.
*Andrena** sp.	Michener 1953	Arnett 1985	1346.
Panurgus sp.	Saunders 1891; DeMoll 1908; [Plant & Paulus 1987]	[Step 1932]; Richards & Davies 1977	1347.
Oxaeidae			
*Protoxaea gloriosa** Fox	Rozen 1964	Rozen 1964	1348.
Melittidae			
Macropis sp.	Saunders 1891; Stephen, Bohart & Torchio 1969	[Arnett 1985]	1349.
Megachilidae			
Anthidium atripes Cresson	Saunders 1981; Michener 1944; Stephen, Bohart & Torchio 1969; Winston 1979	Michener 1944; Arnett 1985	1350.
*Fidelia villosa** Braun	Rozen 1970	Rozen 1970	1351.
Megachile sp.	Saunders 1891; [Stephen, Bohart & Torchio 1969]; [Winston 1979]	Swan & Papp 1972; [Milne & Milne 1980]; [Arnett & Jacques 1981]	1352.
Osmia sp.	Saunders 1891; DeMoll 1908; Nedel 1960; Stephen, Bohart & Torchio 1969; [Plant & Paulus 1987]	[Arnett & Jacques 1981]; Arnett 1985	1353.
Anthophoridae			
Anthophora edwardsii Cresson	[Saunders 1891]; [DeMoll 1908]; Michener 1944; [Stephen, Bohart & Torchio 1969]; [Winston 1979]; [Plant & Paulus 1987]	Swan & Papp 1972; Milne & Milne 1980; [Arnett 1985]	1354.
*Anthophora stanfordiana** Cockerell	Michener 1953	Arnett 1985	1355.
Eucera sp.	Saunders 1891; DeMoll 1908; [Winston 1979]	Barth 1985	1356.
*Triepeolus remigatus** (Fabricius)	[Michener 1953]; Stephen, Bohart & Torchio 1969	Stephen, Bohart & Torchio 1969	1357.
*Xylocopa virginica** (Linneaus)	[Berlese 1909]; [Snodgrass 1947]; Michener 1953	[Arnett & Jacques 1981]; Frankie & Daly 1983	1358.
Apidae			
Apis mellifera Linneaus	Briant 1894; Breithaupt 1886; Saunders 1891; DeMoll 1908; Kellogg 1902; Snodgrass 1928, 1935, 1960; DuPorte 1946, 1957; Costa-Cruz 1962; Ross 1965; Stephen, Bohart & Torchio 1969; Romoser 1973; Atkins 1978; [Winston 1979]; Masuko 1986; [Plant & Paulus 1987]	Milne & Milne 1980; Arnett & Jacques 1981	1359.

taxon	mouthpart-morphology data	dietary data	no.
_Apis mellifera_* Linneaus	Nelson 1924; Peterson 1948; Michener 1953; Stephen, Bohart & Torchio 1969	Peterson 1948; Richards & Davies 1977	1360.
_Bombus americanorum_* Fabricius	[Short 1952]; Michener 1953; Stephen, Bohart & Torchio 1969	[Arnett & Jacques 1981]	1361.
Bombus vosnesenskii Radoszkowski	[Kraepelin 1882]; Saunders 1891; [Smith 1898]; Michener 1944; Nedel 1960; Stephen, Bohart & Torchio 1969; [Winston 1979]; [Harder 1981]; [Plant & Paulus 1987]	[Arnett & Jacques 1981]; Heithaus 1983	1362.
Psithyrus sp.	Saunders 1891; Liu 1925; Stephen Bohart & Torchio 1969	Arnett 1985	1363.
_Trigona cupira_* Smith	Michener 1953	[Johnson 1983]	1364.
Trigona scaptotrigona	Nedel 1960; Kerr & Costa-Cruz 1961; Costa-Cruz 1962; [Plant & Paulus 1987]	[Costa-Lima 1968]; [Johnson 1983]; Barth 1985	1365.

APPENDIX C

DATA ENTRIES OF MOUTHPART MORPHOLOGY CHARACTER-STATES FOR RECENT INSECT SPECIES*

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
1.	PRO	*Acerentomon affine*	CCBCAAAE	ACA	FBGBCB	DC	BBDG	BGD	BKBDF	CCGEFCDFF	DCFCJPKDG	BNDEEFA
2.	PRO	*Acerentulus tiarneus*	CCBCAAAE	AAA	FBGBCB	DC	CBEG	BGD	BKBDF	CCGDFDDFF	DCFBJPKDG	BNDBEFA
3.	PRO	*Eosentomon transitorium*	CBBBAAAE	AAA	FBFBCB	DB	CBEG	BEB	BKBDF	DCGEFDIFF	DCFCJPKDG	BNDBEFA
4.	COM	*Onychiurus armatus*	CAABAAAA	CEA	FAABFA	DB	CBEA	CDB	BQCBA	DCGBIBBLA	DBBAAHAAG	EUDEDFA
5.	COM	*Orchesella cincta*	CABBAAAA	CED	FAABCA	DB	CBBA	CCG	BQEBA	DCGBJDBJA	DCEBJAADG	EZADDFA
6.	COM	*Folsomia candida*	CAABAAAA	CEA	FAABBA	BC	CBBA	CDE	BQEBA	DCGCGDILA	DCBAAHAAG	EVCEDFA
7.	COM	*Tomocerus plumbeus*	CABBAAAA	CED	FAABCA	DC	CBBA	CCE	BQEBA	DCGCJDBJA	DCBAAHAAG	ELCDDFA
8.	COM	*Brachystomella parvula*	CABBAAAA	MED	FAABDA	CB	CBBC	CFE	BAAAA	DDEAAABLE	DBFDEHADB	L*CEEFA
9.	COM	*Anurida maritima*	CABBAAAA	MED	FAABCA	DB	CBGA	CCE	BQDBA	DCEAAAIKA	DCBAAHAAA	CWBDCFA
10.	COM	*Neanura muscorum*	CCBCAAAA	CED	FBCBCB	DC	BBDA	BCF	BQDDF	DCCAAAAEF	DCBAABBAG	BLCEDFA
11.	COM	*Deuterosminthurus 5-fasciatus*	CABBAAAA	IED	FAAACA		CBGA	CCE	BQEBA	CCCAAAALA	DCBAAHAAG	EUCDDFA
12.	DPL	*Campodea chardardi*	CAACAAAA	DAA	FAABCA	DB	CBBA	CDE	BQDBA	CCGBJDBKA	DCFBJBBDG	DUCDDFA
13.	DPL	*Heterojapyx gallardi*	CAACAAAD	DAA	FAABFA	DB	CBBA	CCE	BQDBA	CCGDBCBMA	CCFCBBBCG	EQCDDFA
14.	DPL	*Japyx major*	CAACAAAD	DAA	FAABFA	DB	CBBA	CBE	BQDBA	CCGDBDINA	CCGBJJCDG	EQCDDFA
15.	ARC	*Machilus* sp.	CBCAAAAC	BEB	CAABAA	CB	CBBA	CDB	BQEBA	BCGGBBBJA	DDGDBB CA	EVCDDFA
16.	ARC	*Petrobius brevistylus*	CBCAAAAC	BEB	CAABDA	CB	CBBA	CDH	BQEBA	CCGGBBBNA	DDGDCICCA	E*ADDFA
17.	ARC	*Nesomachilus maoricus*	CBCAAAAC	BAB	CAABDA	CB	CBBA	CDH	BQEBA	CCGGBBBKA	DDGDCI CA	EVCDDFA
18.	TYN	*Tricholepidion gertschi*	CBBCAAAA	BDD	CAABFA	DB	BBBA	CBE	CBEBA	BCGFCEJKA	BCGECHCCA	EUCDEFA
19.	TYN	*Acrotelsa collaris*	CAACAAAA	CAA	CAABFA	DC	CBBA	CEE	CDDBA	CCGFCBBMA	ECGDCBBCA	EVCDDFA
20.	TYN	*Ctenolepisma longicaudata*	CAACAAAA	CAA	CAABFA	DC	CBBA	CEE	CDDBA	CCGFBBBNA	ECGDCBBCA	EACDDFA
21.	TYN	*Lepisma* sp.	CACCAAAA	CAD	CAABFA	DB	DBBA	CBE	CDDBA	CBGFBCBNA	ECGDCBFCA	EZCDDFA
22.	TYN	*Thermobia domestica*	CACCAAAA	CAD	CAABFA	DB	DBBA	CBE	CDDBA	CBGFBBMMA	ECGDCFFBA	EZCDDFA
23.	TYN	*Protrinemura mediterranea*	CAACAAAA	BAA	CAABFA	CB	CBGA	CBE	CDDBA	CCGFCEPKA	DCGDCFFCA	EUCDDFC
24.	EPH	*Ameletus inopinatus**	CABAAAAA	BDB	BAACFA	DC	CBCA	CDE	CBEBA	CCGDBBIBA	DCGDBCCCA	EACDBBA
25.	EPH	*Siphloneurus lacustrus**	CABAAAAI	BDB	BAACCA	CC	CBCA	CFE	CCFBA	CBHDBCNQA	DCGDCCCCA	L*CCBBA
26.	EPH	*Ametropus fragilis**	BABAAAAI	BDD	CAACCA	CB	DBCA	CFC	CCFBA	CDHDBCNQA	DCGD HJCA	L*CCBBA
27.	EPH	*Baetis rhodani**	BABAAAAA	BDC	CAACCA	CB	CBCA	CFB	CCFBA	CCHCBCNQA	DBGDCFJCA	G*CCBBC
28.	EPH	*Chloeon dipterum**	CABAAAAA	BDC	CAACCA	DB	CBCA	CDC	CCFBA	CCHDBBNQA	DCGDCHFDA	G*CCBBC
29.	EPH	*Oligoneuriella rhenana**	CABAAAAI	BDD	CAACCA	B	CBNA	CFC	CCFBA	CBGCBCI A	DCGC CA	L*CCBBA
30.	EPH	*Isonychia ignota**	CABAAAAI	BDB	BAACFA	CC	CBGA	CDE	CBEBA	CCGCGCI A	DCGCECCCA	L*CCBBA
31.	EPH	*Arthroplea congener**	CABAAAAI	BDD	CAACAA	DB	DBBA	CCC	CCFBA	CCHCGBNQA	DCGCEHJCA	M*CCBBA
32.	EPH	*Ecdyonurus helveticus**	CABAAAAI	BDD	CAACCA	CB	DBGA	CFE	CCFBA	CCHCGCNQA	DCGCEHJDA	M*CCBBA

---

*Asterisks after some Latin binomens designate immature stages (i.e. nymphs, naiads, or larvae)

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
33.	EPH	_Ecdyurus*_ sp.	CABAAAAI	BDD	CAACCA	CB	DBGA	CFC	CCFBA	CCHCGBNQA	DCGCEHJCA	M*CCBBA
34.	EPH	_Heptagenia flava*_	CABAAAAI	BDD	CAACCA	CB	DGBA	CFC	CCFBA	BCHCGCNQA	DCGCFHJDA	M*CCBBA
35.	EPH	_Lepeorus goyi*_	CABAAAAI	BDD	CAACCA	DB	DBGA	CFC	CBFBA	CCHDGCHJA	DCGDELJCA	M*CCBBA
36.	EPH	_Stenonema vicarium*_	CABAAAAI	BDD	CAACCA	BC	CBGA	CFC	CCFBA	CBHCGCNQA	DCGCFHJDA	M*CCBBA
37.	EPH	_Stenonema vicarium_	BBCAAAAA	BDB	CGACAA	CB	CBBA	CCA	CABAA	BBFCJDAAA	DBEBJAADA	QZEAEFC
38.	EPH	_Habroleptoides modesta*_	BABAAAAI	BDD	CAACCA	DB	CBCA	CFC	CCFBA	CBHDGCNQA	DCGDEHICA	M*CCBBA
39.	EPH	_Leptophlebia*_ sp.	CACAAAAI	BDD	CAACCA	DB	CBBA	CFC	CCFBA	CBHDGBNQA	DCGDEHJCA	M*CCBBA
40.	EPH	_Paraleptophlebia submarginata*_	BACAAAAI	BDD	CAACCA	CB	CBBA	CFC	CCFBA	CCHDGBNQA	DCGDEHICA	M*CCBBA
41.	EPH	_Rithrogenia*_ sp.	CACAAAAI	BDD	CAACCA	CB	CBBA	CFC	CCFBA	CBHDGCNQA	DBGDEHJCA	M*CCBBA
42.	EPH	_Behningia ulmeri*_	CACAAAAC	BDD	CAABFA	CB	DBGA	CDC	CDFBA	BBHCSBNQA	DBGCEFICA	M*CCGBA
43.	EPH	_Potamanthus luteus*_	CACAAAAI	BDD	BAACFA	DC	DBGA	CFC	CCDBA	BBHDGCNQA	DCFDEHICA	L*CCBBA
44.	EPH	_Ephoron virgo*_	CBCAAAAI	BDD	BAACAA	CB	CBGA	CPH	CFFBA	BBHCCCNQA	DBGCEMICA	M*CCGBA
45.	EPH	_Ephemera vulgata*_	CBCAAAAI	BDD	BAACAA	CB	CBGA	CFB	C JBA	BCHDGBNQA	DCGDEHJCA	M*CCGBA
46.	EPH	_Hexagenia recurvata_	BACAAAAA	BDB	CGACAA	CB	DBBA	CAA	CABAA	BBFBJAAAA	EBEBJAADA	QZEAEFA
47.	EPH	_Hexagenia*_ sp.	CBCAAAAI	BDD	BAACAA	CB	CBGA	CFB	CFJBA	BBHDGBNQA	DBGDEHJCA	M*CCGBA
48.	EPH	_Palingenia longicauda*_	CBCAAAAI	BDB	BAACAA	CB	CBGA	CFB	CHIBA	BBHDGCNQA	DBGCEDICA	M*CCGBA
49.	EPH	_Ephemerella ignita*_	BABAAAAI	BDD	CAACCA	CB	CBGA	CFC	CCFBA	CCHDICNQA	DCGDEHJCA	L*CCBBA
50.	EPH	_Caenis macrura*_	BABAAAAI	BDD	CAACCA	CB	DBBA	CFC	CCFBA	CBHDGCNQA	DCGDEHJCA	L*CCBBA
51.	EPH	_Prosopistoma foliaceum*_	CABAAAAA	BDD	CAABFA	DB	DBBA	CBE	CBDBA	BCHDBCNQA	DBFDBJICA	GQCDBBA
52.	ODO	_Lestes barbarus_	BBCCABAB	BDB	CAABCA	DC	BBBA	CBE	CBDBA	CEHBKCNQA	DCFCMJHDA	EQCDEFA
53.	ODO	_Agrion hastulatum*_	BDCAAAAA	BDD	BAABCA	CC	BBGH	CBE	CDDBA	CCHBKCNQA	BCFCGJHCF	EQCDBBA
54.	ODO	_Pseudagrion decorum_	BBCCABAB	BDB	CAABCA	DC	CBBA	CBE	CBDBA	CEHBKCNQA	DCFCMJHDA	EQCDEFA
55.	ODO	_Mnais strigata_	BBCCABAB	BDB	CAABCA	DC	BBGA	CBE	CBDBA	CEHBKCNQA	DCFCMJHDA	EQCDEFA
56.	ODO	_Epiophlebia superstes*_	CDCAAAAA	BDB	BAABCA	CC	BBGH	CBE	CDDBA	CCHBKDNQA	BCFCGJHCF	EQCDBBA
57.	ODO	_Epiophlebia superstes_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBE	CBDBA	GEHBKCNQA	DCFCMJHDA	EQCDEFA
58.	ODO	_Davidius nanus_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBE	CBDBA	CEHBKDNQA	DCFCMJHDA	EQCDEFA
59.	ODO	_Gomphus agricola_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBE	CBDBA	CEHBKCNQA	DCFCMJHDA	EQCDEFA
60.	ODO	_Ictinogomphus rapax_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBE	CBDBA	CEHBKCNQA	DCFCMJHDA	EQCDEFA
61.	ODO	_Ictinus angulosus_	CBCCAAAB	BDB	CAABCA	CC	CBGA	CBE	CBEBA	CBHBKBNQA	CCFCMJHDA	EQCDDFA
62.	ODO	_Onychogomphus ardens_	CBCCAAAB	BDB	CAABCA	DC	CBGA	CBC	CBDBA	CEHBKCNQA	DCFCMJHDA	EQCDEFA
63.	ODO	_Aeshna cyanea*_	CDCAAAAA	BDB	BAABCA	DC	BBSH	CBE	CDDBA	CCHBKCNQA	BCFCGJHCF	EQCDBBA
64.	ODO	_Aeshna juncea_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBC	CBDBA	CEHBKCNQA	DCFCMJHDA	EQCDEFA
65.	ODO	_Anax junius*_	CDCAAAAA	BDB	BAABCA	DC	BBGH	CBE	CDDBA	CCHBKBNQA	BCFCGJHCF	EQCDBBA
66.	ODO	_Anax junius_	CBCCAAAB	BDB	CAABCA	CC	BBGA	CBE	CBDBA	CEHBKCNQA	DCFCMJHDA	EQCDEFA
67.	ODO	_Cordulegaster boltoni_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBH	CBDBA	CCHBKCNQA	DCFCMJHDA	EQCDEFA
68.	ODO	_Brachythemis contaminata_	CBCCAAAB	BDB	CAABCA	DC	BBBA	CBE	CBDBA	CEHBKCNQA	DCFBMJHDA	EQCDEFA
69.	ODO	_Crocothemis servilia_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBE	CBMBA	CEHBKCNQA	DCFBMJHDA	EQCDEFA
70.	ODO	_Libellula quadrimaculata*_	CCCCAAAA	BDD	BAABCA	DC	BBGH	CBC	CDDBA	CCHBKCDQA	CCFCGJHDF	EQCDBBA
71.	ODO	_Libellula quadrimaculata_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBC	CBDBA	CEHBKCNQA	CCFBMJHDA	EQCDEFA
72.	ODO	_Orthetrum taeniolatum_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBC	CBDBA	BEHBKCNQA	DCFBMJHDA	EQCDEFA
73.	ODO	_Pantala flavescens_	CBCCAAAB	BDB	CAABCA	DC	BBGA	CBC	CBDBA	CEHBKCNQA	DCFBMJHDA	EQCDEFA
74.	BLA	_Cryptocerus punctulatus_	CBCAAAAC	BCD	CAACCA	DB	CBBA	CBE	CBDBA	CCGFCBMKA	CCGDCCBCA	EKCDDFA
75.	BLA	_Blatta orientalis_	CBBAAAAC	BCD	CAABBA	DC	DBBA	CBE	CBEBA	CEGECBMKA	CDGDDEBCA	DUCDDFA
76.	BLA	_Periplaneta australasiae_	CBCAAAAC	BCD	CAABBA	DC	CBCA	CBE	CBEBA	CEGFCBMKA	DDGDDEBBA	DUCDDFA
77.	BLA	_Blatella germanica_	CBCAAAAC	BCD	CAABBA	DB	CBCA	CBE	CBEBA	BEGFCBMKA	DDGDDEBCA	D&CDDFA
78.	BLA	_Parcoblatta pensylvanica_	CBCAAAAC	BCD	CAABBA	CB	CBBA	CBE	CBEBA	CEGFCBMKA	DDGDDEBCA	D&CDDFA
79.	BLA	_Blaberus cranifer_	CBBBAAAC	BCB	CAABCA	CB	CBBA	CBE	CBDBA	CCGFCEMKA	CCSDDBBCA	EWCDDFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
80.	MAN	*Eremiaphila* sp.	CBCAAAAB	CDB	CAABCA	CB	CBBA	CBE	CBDBA	CEGFCBMKA	DDSDDBBBA	EQCDEFA
81.	MAN	*Mantis religiosa*	CBCAAAAB	CDB	CAABCA	CB	CBBA	CBE	CBDBA	CEGFCBMKA	DDGDDFFBA	EQCDEFA
82.	MAN	*Stagnomantis carolina*	CBCAAAAB	CDB	CAABCA	CB	CBBA	CBJ	CBDBA	BEGFCBMKA	DDGDDFFBA	EQCDEFA
83.	MAN	*Tenodera sinensis*	CBCAAAAB	CDB	CAABCA	CB	CBBA	CBC	CBDBA	CEGFCBMKA	DDGDDBBBA	EQCDEFA
84.	ISO	*Mastotermes darwinensis*	CBCBAAAA	DCB	BAACBA	DC	CBBA	CBE	CDEBA	CEGFCBMKA	CCGDDFCCA	EKCDDFB
85.	ISO	*Kalotermes flavicollis*	CBABAAAA	DCA	BAABBA	DC	CBBA	CBC	CDEBA	CEGFCCMKA	CCGDDBCDA	EKCDECC
86.	ISO	*Archotermopsis* sp.	CBABAAAA	DCA	BAABBA	DC	CBBA	CBE	CFBBA	CEGFCBMKA	CCGDDBCCA	EZBEDFD
87.	ISO	*Termopsis* sp.	CBCBAAAA	DAD	BAABCA	DC	CBBA	CBE	CFBBA	CEGFCCMKA	CCGDDBCBA	EZCEDFD
88.	ISO	*Zootermopsis angusticollis*	CBCBAAAA	DAD	BAABCA	DC	CBBA	CBE	CDEBA	CEGFCCMKA	CCGDDBCBA	EZCDDFA
89.	ISO	*Rhinotermes taurus*	CBCBAAAA	DCB	BAACBA	CC	CBBA	CBE	CDEBA	CEGFCCMKA	DCGDDBC A	EKCDGFA
90.	ISO	*Serritermes serrifer*	DCCBAAAA	CBD	BAACCA	CB	CBEA	CBE	CGIBA	CEHECBDGA	DCGCDCBCA	EUCDDFD
91.	ISO	*Macrotermes gilvus*	DCBCBAAA	DCB	BAABBA	CC	CBBA	CBE	CBEBA	CEGFCCMKA	CCGDDBC A	ENADGFA
92.	ISO	*Nasutitermes chaquimayensis*	CBCBAAAA	DCB	BAACBA	CC	CBBA	CBE	CDEBA	CEGFCBMKA	DCGDDBCBA	EKCDGFD
93.	ISO	*Odontotermes obesus* (alate)	CBCBAAAA	DCB	BAACBA	CC	CBBA	CBJ	CDEBA	CEGFCCMKA	DCGDDBCCA	ENCDGFB
94.	ISO	*Odontotermes obesus* (worker)	CBABAAAA	DAA	BAACBA	CC	CBBA	CBJ	CDEBA	CEGFCCMKA	DCGDDBCCA	EKCDGFC
95.	ISO	*Odontotermes obesus* (soldier)	DBABAAAA	DAA	BAABBA	DC	CBEA	CBE	CFBBA	CEGFCCMKA	CCGDDBCBA	ENCEGFD
96.	GRY	*Grylloblatta campodeiformis*	CBCAAAAA	CAA	BAABCA	DC	CBKA	CBB	CBDBA	BEGFCBFKA	DDGDDFCBA	EQCDDFA
97.	ORT	*Stenopelmatus* sp.	CBBAAAAA	CAD	CAABCA	CC	CBBA	CBE	CBEBA	BEGFCBFKA	DDGDDCCBA	EQCDGFA
98.	ORT	*Cooloola propator*	EBBBAAAA	CDD	CBCBCA	CE	CBBA	BBI	CBIBA	CEGFCEGDF	CDGDDCCCA	UJQBGFC
99.	ORT	*Gryllacris leefmansi*	CBDBAAAA	BAD	CAABCA		CBBA	CBE	CBDBA	CEGFCEFCA	DCGDCCCBA	EQCDEFA
100.	ORT	*Macropathus filifer*	CBBAAAAA	CBD	CAABCA	DC	CBCA	CBI	CBDBA	BDGFCEFKA	CDGDCCCBA	EUCDDFA
101.	ORT	*Tachycines asynamorus*	CBBAAAAA	CDD	CAABCA	CB	CBBA	CBE	CBDBA	BEGFCEFKA	DDGDDFCBA	EUCDDFA
102.	ORT	*Cyphoderris* sp.	CBBBAAAA	BBD	CAABCA	BC	CBBA	CBE	CFDBA	CCGECBFCA	CCGDDCCBA	EQCDDFC
103.	ORT	*Amblycorypha oblongifolia*	CBBAAAAA	CDD	CAABCA	CB	CBBA	CBE	CBDBA	BEGFCEGKA	DDGDDFCBA	EECDEFA
104.	ORT	*Mecopoda elongata*	CBBBAAAA	BDB	CAACCA		CBBA	CBE	CBEBA	BDGFCEFCA	CCGDDCCBA	EECDEFC
105.	ORT	*Dectius albifrons*	CBBAAAAA	CDD	CAABCA	CC	CBCA	CBE	CBDBA	BEGFCEFKA	CDGDDFCBA	EECDEFA
106.	ORT	*Saga serrata*	DBDAAAAA	CDD	CAABCA	CB	CBBA	CBE	CBDBA	BEGFCBFKA	DDGDDFCBA	EQPDEDA
107.	ORT	*Orchelimum vulgare*	CBDAAAAA	CDD	CAABCA	CB	CBBA	CBE	CBEBA	BEGFCEFKA	DDGDDFCBA	EEBDEFA
108.	ORT	*Gryllotalpa gryllotalpa*	CBCAAAAA	DCD	BAABCA	DC	CBBA	CBE	CBDBA	CEGFCBFKA	DDGDDFCBA	EJCDGFA
109.	ORT	*Acheta domestica*	CBCAAAAA	CDB	CFABBB	CC	CBBA	CIN	CBDBA	BEGFCEFKC	DDGDDFCBA	H&CEDFA
110.	ORT	*Gryllus pennsylvanicus*	CBCAAAAA	CDB	CFABBB	DC	CBBA	CIN	CBDBA	BEGFDEFKC	DDGDCFCBA	H&CEDFA
111.	ORT	*Liogryllus campestris*	CBCAAAAA	CDB	CFABBB	DC	CBBA	CIN	CBDBA	CEGFCEFKC	DDGDCFCBA	H&CEDFA
112.	ORT	*Luzara minor*	CBBCAAAA	BDB	CFABBB	DC	CBBA	CIE	CBDBA	BDGFDEFKC	DDGDDFCBA	H&CDFFC
113.	ORT	*Myrmecophila acevorum*	CBBCAAAA	BAD	CFABBB	CC	CBMA	CIE	CBDBA	BCGFCBFMC	CDGDDCCBA	H&CDDFA
114.	ORT	*Keyacris scurra*	DBDAAAAA	FDB	DAACCA	DB	CBCA	CBK	CBEBA	BEGFCBMMA	CDGDDMBBA	EECDEFA
115.	ORT	*Cephalocoema albrechti*	EBDCACAA	CBB	DAACCA	DB	CBCA	CCG	CDEBA	GEGFCBMMA	CCGDDMBBA	EACDEFA
116.	ORT	*Tanaocerus koebelei*	CBDAAAAA	BDB	CAACCA	DB	BBBA	CBE	CDEBA	BEGFCCBBA	CCGDDBBCA	EECDLFC
117.	ORT	*Bullacris unicolor*	CBDCAAAA	CDD	CAACCA	DB	BBCA	CBE	CDEBA	CDGECBEKA	DDGDDMIBA	EACDEFC
118.	ORT	*Zonocerus variegatus*	CBDCAAAA	BDD	CAACCA	CB	CBCA	CBC	CDLBA	BDGECBFMA	CCGDDMICA	EECDEFA
119.	ORT	*Ommexecha brunneri*	CBDCAAAA	BDB	CAACCA	CB	BBBA	C	CDEBA	CEGECBBBA	CCGCDBBBA	EECDEFA
120.	ORT	*Romalea microptera*	CBDAAAAA	CDD	CAABCA	DC	DBCA	CBC	CBCBA	BEGFCBFKA	DDGDDMIBA	EECDEFA
121.	ORT	*Marellia remipes*	CBDAAAAA	CDD	CAACCA	DC	CBCA	CBC	CBEBA	BEGFCBFKA	DDGDDMIBA	EECDEFA
122.	ORT	*Anacrydium aegyptium*	CBDAAAAA	CDD	CAABCA	DC	CBBA	CBE	CBCBA	BEGFCBFKA	DDCDDAIBA	FDCEDFA
123.	ORT	*Dissosteira carolina*	CBDAAAAA	CDD	CAACCA	DC	DBCA	CBC	CBCBA	BEGFCEFKA	DDGDDMIBA	FDBDEFA
124.	ORT	*Hippiscus* sp.	CBDAAAAA	CDD	CAACCA	C	CBCA	CBC	CBCBA	BEGFCBFKA	DDCDDAIBA	FDBDEFA
125.	ORT	*Locusta migratoria*	CBBAAAAA	CDD	CAACCA	CC	CBCA	CBE	CDEBA	BEGFCBFKA	DDGDDCCBA	FDCDEFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
126.	ORT	*Melanopus differentialis*	CBDAAAAA	CDD	CAABCA	DC	CBCA	CBC	CBCBA	BEGFCBFKA	DDGDDMIBA	FDBDEFA
127.	ORT	*Schistocera gregaria*	CBBAAAAA	CDD	CAABCA	DB	CBCA	CBE	CDEBA	BEGFCBFKA	DDGDDB BA	EECDEFA
128.	ORT	*Tryxalis nasuta*	EBDAAAAA	DD	CAABCA	DC	CBBA	CBC	CDCBA	BEGFCBFKA	DDCDDAICA	EEBDEFA
129.	ORT	*Xenocheila zarundyni*	CBBAAAAA	BDB	CAACCA	DB	BBCA	CBN	CBLBA	BCGFCBMLA	CCGDDMCCA	EAADEFA
130.	ORT	*Tetrix arenosus*	CBDAAAAA	CDD	CAABCA	DC	CBBA	CBC	CBEBA	BEGFCBFKA	DDGDDFICA	EACDEFA
131.	ORT	*Tridactylis apicalis*	CBCAAAAA	CDD	CAACCA	DC	CBBA	CBJ	CBEBA	BEGFCBFKA	DDGDDFCCA	EJCDCFA
132.	ORT	*Cylindroryctes spegazzinii*	CBCBAABA	FAA	BAABCA	DB	BBGA	CBE	CBEBA	CCGFCBFKA	CCGDDCCCA	EJCDGFA
133.	PHA	*Timema* sp.	CBBCAAAA	DCD	BAABCA	DB	DBCA	CBA	CDCBA	BEGFCCMKA	DDGDDCCCA	EECDEFB
134.	PHA	*Anisomorpha ferruginea*	DBCCAAAA	CCD	BAABCA	DB	CBCA	CBH	CDCBA	BEGFCBMKA	DDGDDCCBA	EEBDEFA
135.	PHA	*Necrosia sparaxes*	CBCCAAAA	CCD	BAABCA	DB	CBCA	CBA	CDCBA	BEGFCBMKA	DDGDDCCCA	EECDEFB
136.	PHA	*Diaphanomera femorata*	DBCCAAAA	CCD	BAABCA	DB	DBCA	CBA	CDCBA	BEGFCBLKA	CDGDDCCBA	EEBDEFA
137.	PHA	*Carausius morosus*	DBCCAAAA	CCD	BAABCA	DB	DBCA	CBE	CDCBA	BEGFCBMKA	DDGDDCCBA	EECDEFA
138.	PHA	*Phryganistra virgea*	DBCCAAAA	CCD	BAABCA	DB	CBCA	CBA	CDCBA	BEGFCBMKA	DDGDDFCBA	EECDEFA
139.	DER	*Echinosoma afrum*	CBCCAAAD	CAD	BAABCA	DC	DBKA	CDE	CBEBA	CEGFCBGKA	DDCDDACCA	EQCDDFA
140.	DER	*Anisolabis maritima*	CBCCAAAD	CAD	BAABCA	DC	CBGA	CDC	CBEBA	CEGFCBGKA	DDCDDAJCA	EZCDDFA
141.	DER	*Labidura riparia*	CBCCAAAD	CAD	BAABCA	CC	CBGA	CDC	CBDBA	CEGFCBMKA	DDCDDACCA	EQCDDFA
142.	DER	*Forficula auricularia*	CBCCAAAD	CAD	BAABCA	DC	CBBA	CDC	CBEBA	CEGFCBGKA	DDCDDACBA	EACDEFA
143.	DER	*Hemimerus talpoides*	BBCCAAAA	CAA	BAABCA	D	DBGA	CDD	CBDBA	BEGFCCDKA	DCCDDACCA	DTABFFA
144.	DER	*Arixenia esau*	CBCCAAAA	CAA	BAABCA	DC	CBBA	CDC	CBFBA	CEGFCBIKA	DDCDDACCA	GTABFFA
145.	EMB	*Embia ramburi*	CBCCAAAA	CAD	BAABCA	DC	DBBA	CBE	CBDBA	BEGFCBBKA	DDGDDNCCA	EVCDEFA
146.	EMB	*Notoligotoma hardyi*	CBCBAAAA	CAD	BAACCA	DB	BBBG	CBC	CFDBA	BCGFCBBKA	CCGDDNCCA	EUCEGFC
147.	EMB	*Embolyntha batesi*	CBCCAAAA	CAD	BAABCA	DC	DBBA	CBE	CDDBA	BEGFCCBCA	DDGDDNCCA	EACDDFA
148.	EMB	*Anisembia* sp.	CBCCAAAA	CAD	BAABCA	DB	BBGA	CBC	CBDBA	CCGFCBBKA	DCGDDNCCA	EUCEGFB
149.	EMB	*Australembia incompta*	CBCBAAAA	CAD	BAABCA	BB	BBBA	CBE	CFDBA	DCGFCBGMA	DDCDDACCA	EVCEDFC
150.	EMB	*Oligotoma hospes*	CBCCAAAA	CAD	BAABCA	DC	DBGA	CBE	CBDBA	BEGFCBBKA	DDGDDMICA	EJBDDFA
151.	EMB	*Teratembia geniculata*	CBBBAAAA	CAD	BAABCA	DB	BBBA	CBE	CBDBA	CEGFDCBKA	CCGDDNCCA	EVCDGFC
152.	PLE	*Nemoura varigata*	CBCAAAAA	BDD	BAABAA	DB	DBBA	CBC	CBDAA	BEGFCBPKA	DDGDOFIDA	QZEAEFA
153.	PLE	*Nemoura venosa**	CBCAAAAA	BDD	BAACCA	DB	CBGA	CBC	CBLBA	CEGFCCPKA	DDGDOBJDA	EVCDBBA
154.	PLE	*Notonemoura latipennis**	CBBCAAAA	BDD	BAABCA	CB	BBBA	CBC	CBEBA	CEGFCBPNA	DCGDDCCCA	EACCBBA
155.	PLE	*Capnia necydaloides*	CBCAAAAA	BDD	BAABAA	DB	DBBA	CBC	CDBAA	BEGFCBPNA	DDGDOBBDA	QZEAEFA
156.	PLE	*Capnia vernalis**	CBCAAAAA	BDD	BAABCA	DB	DBGA	CBC	CBDBA	CEGFCCPKA	DDGDOBCDA	EECDBBA
157.	PLE	*Leuctra klapaleki**	CBCAAAAA	BDD	BAACCA	DB	DBGA	CBC	CBLBA	BEGFCBPKA	DDGDOBJCA	EECDBBA
158.	PLE	*Leuctra* sp.	CBCAAAAA	BDD	BAACAA	DB	DBGA	CBC	CBLBA	CEGFCBPKA	DDGDOBCDA	QZEAEFA
159.	PLE	*Taeniopteryx frigidus**	CBCAAAAA	BDD	BAABCA	CB	CBGA	CBC	CBEBA	CDGFCCPKA	DDGDOBFCA	EECDBBA
160.	PLE	*Taeniopteryx frigidus*	CBCAAAAA	BDD	BAACCA	CB	DBGA	CBC	CBDBA	CEGFCCPKA	DDGDOBBCA	EFDDEFA
161.	PLE	*Acroneuria abnormis*	CBCAAAAA	BDD	BAABAA	DB	DBGA	CBC	CMBAA	CEGFCBFKA	DDGDDOCBA	QZEAEFA
162.	PLE	*Acroneuria pacifica**	CBCAAAAA	BDD	BAABCA	DB	DCGA	CBC	CFDBA	CEGFBBGKA	DDGDDOCBA	EQDDBBA
163.	PLE	*Perla cephalotes**	CBCAAAAA	BDD	BAABCA	DB	DCGA	CBC	CFLBA	BEGFCBPKA	ECGDDOJBA	EQCDBBA
164.	PLE	*Perla maxima*	CBCAAAAA	BDD	BAACAA	D	DBBA	CBC	CMBAA	BEGFBBPBA	ECGDDFCBA	QZEAEFA
165.	PLE	*Perlesta placida**	CBCAAAAA	BDD	BAACCA	D	DBGA	CBC	CFLBA	CEGFBBPFA	ECGDDFCBA	EQCDBBA
166.	PLE	*Perlesta placida*	CBCAAAAA	BDD	BAABAA	D	DBBA	CBC	CMBAA	BEGFCBPRA	DCGDDFCCA	QZEAEFA
167.	PLE	*Perlodes tibialis**	CBCAAAAA	BDD	BAABCA	D	DBGA	CBC	CFLBA	CEGFBBGKA	DCGDDBCBA	EQCDBBA
168.	PLE	*Alloperla minuta**	CBCAAAAA	BDD	BAABCA	D	DBGA	CBC	CFLBA	CEGFCCPKA	DCGDDMJCA	EQCDBBA
169.	PLE	*Alloperla minuta*	CBCAAAAA	BDD	BAABAA	D	DBBA	CBC	CMBAA	BEGFCBPRA	DDGDDFCCA	QZEAEFA
170.	PLE	*Chloroperla cydippe**	CBCAAAAA	BDD	BAABCA	D	DBGA	CBC	CFLBA	CEGFCCPKA	DCGDDMCCA	EQCDBBA

	order	taxon	mouthpart morphology data									dietary
			I	II	III	IV	V	VI	VII	VIII	IX	data
171.	PLE	_Chloroperla grammatica_	CBCAAAAA	BDD	BAABAA	DE	DBBA	CBC	CMLAA	BEGFCEPRA	DDGDDMCBA	QZEAEFA
172.	PLE	_Isopteryx tripunctata_	CBCAAAAA	BDD	BAABAA	D	DBBA	CBC	DMLAA	BEGFCBJKA	DCGDDFCCA	QZEAEFA
173.	PLE	_Peltoperla_* sp.	BBCAAAAA	BDD	BAACCA	DB	DBGA	CBC	CBEBA	CDGFCBIKA	DDGDDHJCA	EECDBBA
174.	PLE	_Pteronarcys californica_*	CBCAAAAA	BDD	BAACCA	DB	DBGA	CBC	CBLBA	BEGFCBPKA	DDGDDBCCA	EVCDBBA
175.	PLE	_Pteronarcys regalis_	CBCAAAAA	BDD	BAABAA	CE	DBEA	CBC	CDBAA	BEGFCBPNA	DDGDDBBBA	QZEAEFA
176.	PLE	_Diamphipnoa annulata_*	CBBCAAAA	BDD	BAACCA	DB	BBGA	CBE	CBLBA	BDGECCIKA	CCGDDHJCA	EVCDBCA
177.	PLE	_Neuroperla schedingi_	CBBBAAAA	BDD	BAACCA	DB	BBBA	CBE	CBEBA	CDGECBIKA	CCGDFBBBA	EACDEFA
178.	PLE	_Austroperla_* sp.	CBCAAAAA	BDD	CAABCA	EB	DBBA	CBC	CBEBA	CDGFCBBKA	DDGDDBCCA	EACDBBA
179.	PLE	_Austroperla_ sp.	CBCAAAAA	BDD	CAABCA	DE	DBBA	CBC	CBEBA	CDGFCBBKA	DDGDDBCCA	EACDBFA
180.	PLE	_Perlurgoperla personata_*	BBCAAAAA	BDD	CAACCA	EB	BBBA	CBC	CBDBA	CCGFCCPRA	CCGDDCCCA	EPCDBCC
181.	ZOR	_Zorotypus hubbardi_	CBCAAAAA	DDD	CAABFA	DB	CBBA	CBC	CDEBA	RDGFDBPNA	CCSDCHCCA	EUCEDFA
182.	PSO	_Lepinotus_ sp.	CBBAAAAA	CDD	CAABBA	CC	DBBA	CLJ	CDEBA	BBGEDBGSA	DCGCJKBDA	G&CDDFA
183.	PSO	_Psyllipsocus ramburii_	CBBAAAAA	GDD	CAABBA	CC	DBBA	CLJ	CBEBA	CCGECBFSA	CCGCCKCCA	GUCDDFB
184.	PSO	_Speleketor flocki_	CBBAAAAA	CDD	CAABBA	CC	DBBA	CLJ	CBEBA	CBGECEGSA	DCGCCKCDA	G&CDDFA
185.	PSO	_Prionoglaris latreillei_	CBBAAAAA	CDD	CAABBA	CC	BBBA	CLJ	CDIBA	CCJECBFAA	CCCCDKCCA	GPCDDFB
186.	PSO	_Embidopsocus_ sp.	CBBAAAAA	CAD	CAABBA	CC	DBBA	CLJ	CBEBA	CBGEC GSA	DCGCCKC A	GLCDEFA
187.	PSO	_Stigmatopathus_ sp.	CBDAAAAA	CDD	CAABBA	CC	DBBA	CLJ	CBEBA	CBSEC GSA	DCGCCKC A	G&CDDFA
188.	PSO	_Caecilius maritimus_	CBBAAAAA	CDD	CAABBA	CC	CBBA	CLJ	CBEBA	CCGECBGSA	CCGBJKCCA	GUCDDFC
189.	PSO	_Stenopsocus stigmaticus_	CBBAAAAA	CDB	CAABBA	CC	DBBA	CLJ	CBEBA	BBGECEGSA	DCGBJKC A	G&CDEFA
190.	PSO	_Rhinopsocus arduus_	CBBAAAAA	CDD	CAABBA	CC	BBBA	CLJ	CBEBA	BBGECBGSA	DCGCCKCDA	GVCDDFB
191.	PSO	_Ectopsocus californicus_	CBBAAAAA	CDD	CAABBA	CC	DBBA	CLJ	CBEBA	BBGECEGSA	DCGBJKCDA	GLCDDFA
192.	PSO	_Amphigerontia contaminata_	CBBAAAAA	CDD	CAABBA	CC	DBBA	CLJ	CBEBA	GBGECEGSA	DCGBJBJDA	GLCDEFA
193.	PSO	_Psocus confraternus_	CBBAAAAA	CDB	CAABBA	CC	DBBA	CLJ	CBDBA	BBGECBGSA	DCGBJBJDA	GLCDEFA
194.	ANO	_Haematopinus suis_	DCABAAAA	CAA	FCCBFB	BB	DBKI	AGE	ANBAE	BBBAAAKAA	BDBAADAAB	BRABFFA
195.	ANO	_Neohaematopinus citellinus_	CAABAAAA	CAA	FCCBFB	CB	DBBI	AGE	ANBAE	CBBAAAKAA	BDBAADAAB	BRABFFA
196.	ANO	_Linognathus vituli_	DBABAAAA	CAA	FCCBFB	CB	CBKI	AGE	ANBAE	BBBAAAKAA	BDBAADAAB	BRABFFA
197.	ANO	_Pediculus humanus_	CBABAAAA	CAD	FCCBFB	CB	CBKI	AGE	ANBAE	CBBAAAKAA	BDBAADAAB	BRABFFA
198.	ANO	_Phthirus pubis_	CBABAAAA	CAA	FCCBFB	CB	BBKI	AGE	ANBAE	CBBAAAKAA	BDBAADAAB	BTABFFA
199.	MAL	_Ancistrona vagelli_	BABCAAAA	HAA	BAACBA	DB	DBBA	CLE	CBMBA	CBGEEDSSA	DDCBJACDA	TTADFFA
200.	MAL	_Colpocephalum subaequale_	CABCAAAA	HAA	BAACBA	DB	DBGA	CLE	CBMBA	BBGEECSSA	DDCBJABDA	TTADFFA
201.	MAL	_Myrsidea cornicis_	CABBAAAA	HAA	BAACBA	DB	DBGA	CLE	CBMBA	BBGEECSSA	DDGBJMBDA	TTADFFA
202.	MAL	_Pseudomenopon pilosum_	CABBAAAA	HAA	BAACBA	DB	DBGA	CLE	CBMBA	CBGEECSSA	DDGBJMBDA	TTADFFA
203.	MAL	_Tetrophthalmus_ sp.	CABBAAAA	DAD	CAACBA	DB	BBBA	CLC	CBDBA	CBKECCSSA	CBGBJMFDA	TTAEFFA
204.	MAL	_Laemobothrion gypsis_	CABBAAAA	HAA	BAACBA	DB	DBGA	CLE	CBMBA	CBGEECSSA	DDCBJABDA	TTADFFA
205.	MAL	_Trochiloecetes_ sp.	CABBAPAA	HAA	BBDCBB	DB	DBEA	CGJ	CFDBD	BBGEECSSA	DDDAAJHAA	BRABFFA
206.	MAL	_Heterodoxus spiniger_	CABBAAAA	HAA	BAACBA	DB	DBGA	CLE	CBMBA	BBGEECSSA	DDCBJABDA	TTADFFA
207.	MAL	_Trimenopon jenningsi_	CACBAAAA	HAA	BAACBA	DB	CBGA	CLE	CBMBA	BBGEECSSA	DDGBJMBDA	TTADFFA
208.	MAL	_Gyropus ovalis_	CACBAAAA	HAA	BAACBA	DB	DBGA	CLE	CBMBA	BBGEECSSA	DDGCJMBDA	TTADFFA
209.	MAL	_Bovicola caprae_	CABBAAAA	CAA	CAACBA	DB	DBGA	CLE	CBNBA	BBEAAASSA	DDFBJJHDA	TTADFFA
210.	MAL	_Trichodectes canis_	CABBAAAA	CAA	CAACBA	DB	CBKA	CLJ	CDDBA	BBEAAASSA	DDFBJJHDA	TTADFFA
211.	MAL	_Goniodes lagopi_	CABBAAAA	CAA	CAACBA	DB	DBGA	CLJ	CBMBA	CBEAAASSA	DDFBJJHDA	TTADFFA
212.	MAL	_Philopterus atratus_	CABBAAAA	CAA	CAACBA	CB	CBGA	CLJ	CBNBA	CBEAAAFSA	DDCBJABDA	TTADFFA
213.	MAL	_Cuclotocephalus extraneus_	CABBAAAA	CAD	CAABBA	DB	CBBA	CLE	CDDBA	BBGBJDSSA	BCGCJMFCA	TTAEFFB
214.	MAL	_Haematomyzus elephantis_	DCBBAAAA	FAA	BBBBBB	D	DBCD	AGE	CLICD	CCDAAABDD	CBAAAAAAH	TRABFFA

(HEXASTYLATE, continued)

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
53.	*Eucorethrina flexa* Kalugina	[65]	Kalugina & Kovalev 1985
54.	*Chironomaptera robustus* Lin	[64]	Hong 1983
55.	*Chironomaptera scobloi* Kalugina	[62]	Kalugina & Kovalev 1985
56.	*Chironomaptera collessi* Jell & Duncan	[53]	Jell & Duncan 1986
57.	*Chaoborus tertiarius* (Von Heyden)	[22]	Cook 1981
58.	*Mochlonyx atavus* Loew	[19]	Loew 1861; Larsson 1978
59.	*Chaoborus* sp.	[13]	Cook 1981
60.	*Chaoborus tertiarius* (Von Heyden)	[7]	Statz 1944b
61.	Chaoboridae	[6]	Schumann & Wendt 1989
62.	Culicidae	[57]	Jarzembowski 1984
63.	Culicidae	[23]	Wilson 1978a; Grande 1980
64.	*Culex pipiens* Linneaus	[19]	Keilbach 1982
65.	*Culex protolepis* Cockerell	[18]	Cockerell 1916b
66.	Culicidae	[17]	Schlee & Glockner 1978
67.	Culicidae; *Culicites depereti* Meunier	[15,13]	Wilson 1978a; Lutz 1985
68.	Culicidae	[10]	Cuffey *et al.* 1982
69.	*Anopheles rottensis* Statz	[8]	Statz 1944b
70.	Dixidae	[53]	Jell & Duncan 1986
71.	*Paradixa succinea* Meunier	[19]	Meunier 1906b; Hennig 1966
72.	Dixidae	[6]	Schumann & Wendt 1989
73.	Bibionidae	[76]	Olsen *et al.* 1978
74.	Xylophagidae	[42]	Dmitriev & Zherikin 1988
75.	Stratiomyiidae	[56]	Whalley & Jarzembowski 1985
76.	*Archocyrtus gibbosus* Ussatchov	[60]	Ussatchov 1968
77.	*Archinemestrinus karatavicus* Rohdendorf	[60]	Rohdendorf 1968b
78.	Tabanidae	[24]	Lutz 1987
79.	Tabanidae	[23]	Wilson 1978a; Grande 1980
80.	"*Silvius*" *laticornis* Loew	[19]	Loew 1850; Hennig 1967a
81.	Tabanidae	[17]	Schlee & Glockner 1978
82.	Tabanidae	[15]	Pechuman & Teskey 1981
83.	?Athericidae	[24]	Lutz 1987
84.	*Protobrachyceron liasinum* Handlirsch; *Ija problematica* Kovalev	[68,67]	Handlirsch 1908; Kovalev 1981
85.	*Palaeobrachyceron handlirschi* Kovalev	[66]	Kovalev 1981
86.	*Kubekovia accessoria* Kovalev	[65]	Kalugina & Kovalev 1985
87.	*Palaeoptiolina scobloi* Kovalev	[62]	Kovalev 1982
88.	*Rhagioempis antennata* Rohdendorf	[60]	Rohdendorf 1938; Kovalev 1982
89.	Aff. *Ptiolina*	[57]	Jarzembowski 1984
90.	*Atherimorpha festuca* Jell & Duncan	[53]	Jell & Duncan 1986
91.	Rhagionidae	[37]	Zherikin & Sukacheva 1973
92.	*Protovermileo electricus* Hennig	[19]	Hennig 1967a
93.	*Symphoromyia subtrita* Cockerell	[15]	Cockerell 1911
94.	*Rhagio primaevis* Théobald	[13]	Théobald 1937
95.	Rhagionidae	[6]	Schumann & Wendt 1989
96.	Bombyliidae: *laeoplatypygus zaitzevi* Kovalev	[65]	Kalugina & Kovalev 1985
97.	Empididae: *Protempis antennata* Ussatchov	[60]	Ussatchov 1968

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
263.	HET	*Loricula elegantula*	CDBBBAAA	CAB	ECEBBB	BC	BHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AQBBDFA
264.	HET	*Medocostes lestoni*	CDCBBBAA	CCB	ECEBBA	CC	CBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	AQCBEFB
265.	HET	*Nabis subcoleoptratus*	CCCBCAAB	CCB	ECEBBB	CB	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AQCBEFA
266.	HET	*Plokiophiloides biforis*	CDCBBAAA	CCB	ECEBBB	CB	CBEB	ANH	DIIDG	FBCAAAAEG	CEAAAAAAC	AWCBFFC
267.	HET	*Triphleps insidiosa*	CCBBBAAA	CCB	ECEBBB	BC	CBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	BEABEFA
268.	HET	*Cimex lenticularis*	CDBBCAAC	CAD	ECEBBB	CC	CBHB	ANH	DIIDG	FACAAAAEG	BEAAAAAAC	ARABFFA
269.	HET	*Hesperoctenes cartus*	CCBBAAAG	NAA	CCEBBB	CB	BBBA	ANH	DIBDG	AACAAAAEG	BFAAAAAAC	BTABFFB
270.	HET	*Reduvius personatus*	DCCCCAAA	CCB	ECEBBB	BC	EBHB	ANH	EIIDG	FBCAAAAEG	BEAAAAAAC	AQCBEFA
271.	HET	*Rhodnius prolixus*	DDCBCAAA	CCB	ECEBBB	BC	BBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	ARBBFFA
272.	HET	*Triatoma infestans*	DCCBBAAA	CCB	ECEBBB	BC	BBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	ARBBFFA
273.	HET	*Aradus* sp.	CDBBBAAA	CAD	ECEBBB	CC	CBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	ANCBDFA
274.	HET	*Termititaradus panamensis*	CCABAAAA	CAA	ECEBFB	BB	AAAA	ANH	EIBDG	AACAAAAEG	BEAAAAAAC	ANCBFFA
275.	HET	*Idiostolus insularis*	CDCBBAAA	CCB	ECEBBB	BC	CBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	AIABEFC
276.	HET	*Piesma cinera*	CCCCBAAA	HCD	ECEBBB	BC	BBHB	ANH	DIODG	FBCAAAAEG	CEAAAAAAC	AEABEFA
277.	HET	*Jalysus spinosus*	DCBBBAAA	HCB	ECEBBB	BC	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AEBBEFA
278.	HET	*Neides muticus*	DDBBBAAA	HCB	ECEBBB	BC	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AEBBEFA
279.	HET	*Oncopeltus fasciatus*	CDBBBAAA	CCD	ECEBBB	BC	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	BCABEFA
280.	HET	*Dysdercus cingulatus*	CDBBBAAA	CAD	ECEBBB	BC	EBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	BEABEFA
281.	HET	*Pyrrocoris apterus*	CDBBBAAA	CAD	ECEBBB	BC	EBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	B&ABEFA
282.	HET	*Hyocephalus apragnus*	CDBBBAAA	GCD	ECEBFB	DB	CBEB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	ACCBEFB
283.	HET	*Anasa tristis*	CDBBBAAA	CCD	ECEBBB	BB	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AEBBEFA
284.	HET	*Leptocorisa varicornis*	CDCBBAAA	CCD	ECEBBB	CB	EBHB	ANH	DIBDG	FBCAAAAEG	BEAAAAAAC	ACBBEFA
285.	HET	*Alydus* sp.	CDBBBAAA	CCD	ECEBBB	BC	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AEDBEFA
286.	HET	*Coptosomoides myrmecophilus*	CCCBCAAA	CCD	ECEBBB	BC	DBEB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	ANCBEFA
287.	HET	*Cyrtomenus mirabilis*	CDBBBAAA	CCD	ECEBBB	BC	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AEDBDFA
288.	HET	*Canopus* sp.	CCBBBAAA	CCD	ECEBBB	BB	CBEB	ANH	DIBDG	FBCAAAAEG	BEAAAAAAC	AA BEFA
289.	HET	*Stethaulax marmoratus*	CDBBBAAA	CCB	ECEBBB	BC	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AEBBDFA
290.	HET	*Tessaratoma papillosa*	CCBCBAAA	CCD	ECEBBB	BC	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AEABEFA
291.	HET	*Coridius janus*	CDCBBAAA	CCB	ECEBBB	CC	EBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	AEBBEFA
292.	HET	*Graphosoma lineatum*	CDCBBAAA	CCB	ECEBBB	CC	EBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	AEEBEFA
293.	HET	*Palomena prasina*	CDBCBAAA	CCE	ECEBBB	BC	EBHB	ANH	DIODG	FBCAAAAEG	BEAAAAAAC	AEEBEFA
294.	HOM	*Hemiodoecus leai*	CDBCCAAA	GCD	DCEBBB	CC	DBHB	ANE	EIIDG	FBCAAAAEG	CEAAAAAAC	AVCBDFA
295.	HOM	*Cixius pini*	CCBABAAA	BDD	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
296.	HOM	*Oliarus vicarius*	ECBABAAA	BCB	DCEBBA	BC	BBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
297.	HOM	*Phalix titan*	BCCABAAA	LCD	DCEBBB	CC	CBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AI BEFB
298.	HOM	*Pentagramma vittatifrons*	CCCABAAA	BCB	DCEBBA	CC	CBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AECBEFA
299.	HOM	*Eurybrachys* sp.	CCBABAAA	LCD	DCEBBB	DC	CBEB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AICBEFC
300.	HOM	*Cyropotus reinecki*	CBCABAAA	BCB	DCEBBA	CC	CBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
301.	HOM	*Melicharia quadrata*	EDDACAAA	LCD	DCEBBB	CC	DBHB	ANE	DIBDG	FBCAAAAEG	CEAAAAAAC	AA BEFA
302.	HOM	*Catonia nava*	CCBABAAA	BCB	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
303.	HOM	*Pelitropis rotatula*	CCCABAAA	BCB	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
304.	HOM	*Bruchomorpha* sp.	CBBABAAA	BCB	DCEBBA	CC	CBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
305.	HOM	*Pyrilla perpusilla*	DCCABCAA	BCD	DCEBBB	BC	EBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AAEBEFA
306.	HOM	*Acanalonia latifrons*	CCCABAAA	BCB	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
307.	HOM	*Cyarda melichari*	CCBABAAA	BCB	DCEBBA	C	BBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AECBEFA
308.	HOM	*Flata* sp.	CCBABAAA	BCB	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AECBEFA
309.	HOM	*Amaloptera uhleri*	ECBABAAA	BCB	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
310.	HOM	*Otiocerus degeeri*	ECCABAAA	BCC	DCEBBA	BC	BBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
311.	HOM	*Dictyophara florens*	ECBABAAA	LCB	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	EAAAAAAC	AECBEFA
312.	HOM	*Scolops pungens*	ECCABAAA	LCB	DCEBBA	BC	BBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AECBEFA
313.	HOM	*Bladina synavei*	CCCACCAC	LCD	DCEBBB	CC	EBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AABBEFC
314.	HOM	*Hypochthonella caeca*.	DDCACAAC	LAA	DCEBBB	BB	DBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AJCBGFC
315.	HOM	*Cephiscus siccifolius*	CCBABAAA	BCB	DCEBBA	BC	BBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AECBEFA
316.	HOM	*Lepyronia quadrangularis*. . .	CCBABAAA	BCB	DCEBBA	BC	BBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AECBEFA
317.	HOM	*Magicicada septendecem*. . . .	CDBABAAA	BDB	DCEBBA	BC	BBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AJBBEFA
318.	HOM	*Aulacizes irrorata*.	CCBABAAA	BCB	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	CEAAAAAAC	AECBEFA
319.	HOM	*Idiocerus atkinsoni*	CCBABAAA	BCB	DCEBBA	BC	BBHB	ANE	DIIDG	FBDAAABEG	BEAAAAAAC	AEABEFB
320.	HOM	*Typhlocyba ulmi*	CCBABAAA	BAB	DCEBBA	BC	CBHB	ANE	DIIDG	FBCAAAAEG	CEAAAAAAC	AEABEFA
321.	HOM	*Wolfella caternaulti*.	EDCACAAA	CCB	DCEBBB	BC	DBHB	ANE	DIIDG	FBCAAAAEG	BEAAAAAAC	AICBGFA
322.	HOM	*Entylia sinuata*	CDBABAAA	BCB	DCEBBB	CB	DBEB	ANL	DIICG	FBCAAAAEG	EEAAAAAAC	ADABEFA
323.	HOM	*Eurymeloides pulchra*.	CBBABAAA	BCB	DCEBBA	CC	CBHB	ANE	DIBDG	FBCAAAAEG	CEAAAAAAC	AJBBEFA
324.	HOM	*Stictocephala bubalis*	BCDABAAA	BCB	DCEBBA	CC	BBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AECBEFA
325.	HOM	*Dorthula hardwickii*	CDBACAAA	CCD	DCEBBB	CC	DBHB	ANE	EIIDG	FBCAAAAEG	CEAAAAAAC	AIABEFA
326.	HOM	*Melizoderes darwini*	CDDACAAA	CCB	DCEBBB	BC	DBHB	ANE	DIIDG	FBCAAAAAG	CEAAAAAAC	AIABEFA
327.	HOM	*Psylla mali*	BBBACBAA	CDB	ECEBBA	BC	CBHB	ANE	DIBDG	FDCAAAAEG	DEAAAAAAC	AEABEFA
328.	HOM	*Trialeurodes vaporariorium*. .	CCCABAAA	BCE	ECEBBA	BC	CBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AACBEFA
329.	HOM	*Aphis fabae*	BCBABAAA	CDB	ECEBBA	BC	CBHB	ANE	DIIDG	FBCAAAAEG	BEAAAAAAC	AEBBEFA
330.	HOM	*Eriosoma lanigera*	CCBABAAA	CDB	ECEBBA	CC	CBHB	ANE	DIBDG	FBCAAAAEG	BEAAAAAAC	AJBBEFA
331.	HOM	*Myzus persicae*.	CCBABAAA	CDD	ECEABB	CC	BBHB	ANH	DIIDG	FBCAAAAEG	BEAAAAAAC	AECBEFA
332.	HOM	*Cnapholoides strobilobius**. .	CCCABDAF	OEA	DCEBBA	CC	DBHB	AAA	EIBDG	CBCAAAAEA	CEAAAAAAC	EIABEFB
333.	HOM	*Phylloxera vitifoliae**. . . .	CDAAADAF	FEA	DCEBBB	CC	AAAA	AAA	EIBDG	AACAAAAEG	BEAAAAAAC	AJABGCB
334.	HOM	*Orthezia urticae*.	CABCAABA	CCB	AGABAA	CB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
335.	HOM	*Icerya purchasi*	BACAAABA	CCB	AGABAA		AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
336.	HOM	*Margarodes vitium*	CAAAAABA	CCB	AGABAA	CB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
337.	HOM	*Matsuococcus bisetosus*. . . .	CAAAAABA	CCB	AGABAA	CB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	QZEAEFC
338.	HOM	*Phenacoleachia zealandica* . .	CCBAAABA	CCE	AGABAA	BB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
339.	HOM	*Stictococcus multispinosus** .	CBAAADAF	OCA	DCEBBA	BC	AAAA	AAA	DIIDG	FBCAAAAAG	CEAAAAAAC	AICBEDB
340.	HOM	*Pseudococcus adonidum**. . . .	CBBABDAF	CAD	DCEBBA	CC	CBBA	ANE	DIBDG	FBCAAAAEG	CCAAAAAAC	AJBBECB
341.	HOM	*Coccus hesperidium*.	CABAAABA	CCE	AGABAA		AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
342.	HOM	*Eulecanium tiliae*	CABAAABA	CCE	AGABAA	CB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
343.	HOM	*Physokermes piceae*.	CABAAABA	CCE	AGABAA	CB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
344.	HOM	*Dactylopius austrinus**. . . .	CBAAADAF	OAA	DCEBBA	CB	BBHB	ANE	EIBDG	FBCAAAAEG	BEAAAAAAC	AEABEFB
345.	HOM	*Kermes quercus*.	CAACAABA	DCE	AGABAA		AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
346.	HOM	*Acanthococcus granulatus*. . .	CACAAABA	CCE	AGABAA	DB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
347.	HOM	*Apiomorpha pharetrata*	CACAAABA	CCE	AGABAA	CC	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
348.	HOM	*Laccifer lacca**	CBBABAAA	CAD	DCEBBA	CB	CBBA	ANE	DIBDG	FBCAAAAEG	DCAAAAAAC	AJBBECB
349.	HOM	*Beesonia dipterocarpi**. . . .	CBAAADAF	MAA	DCECBA	CB	BBHB	AAA	EIBDG	FBCAAAAEG	CEEAAAAAC	AEABECB
350.	HOM	*Lecaniodiaspus elytropappi*. .	CABAAABA	CAE	AGABAA	CB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
351.	HOM	*Asterolecanium ungulatum*. . .	CABAAABA	CAE	AGABAA	CB	AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
352.	HOM	*Conchaspis vayssieri*.	CCAAADAF	FCA	DCEBBA	CB	BBHB	AAA	EIBDG	FBCAAAAEG	BEEAAAAAC	AEBBEFB
353.	HOM	*Palmaricococcus nesiotes*. . .	CCAAADAF	NAA	DCEBBA	CB	BBHA	AAA	EIBDG	FBCAAAAEG	CEEAAAAAC	AEABEFB
354.	HOM	*Parlatoria blanchardi**. . . .	CBCABDAF	CDE	DCEBCA	CB	B A	ANJ	DIBDG	FBCAAAAEG	DBAAAAAAC	AJABEFB
355.	HOM	*Quadraspidotus perniciosus*. .	CACAAABA	CCE	AGABAA		AAAA	DAA	AAAAA	AAAAAAAAA	AAAAAAAAA	0ZEAEFC
356.	MEG	*Chauliodes formosanus*	CBCCAAAA	EDD	BAABCA	DB	DBEA	CDE	CFCBA	CCGFCCBBA	CDGDDCBCA	PZEAEFA
357.	MEG	*Chauliodes formosanus**. . . .	CBECABAA	DEA	BAABCA	DC	DBBA	CJB	CFDBA	CCJFCDGAA	DDCDDABDA	EQCDBDA
358.	MEG	*Corydalus cornutus*.	CBCBAAAA	CDD	BAABCA	DB	CBEA	CDE	CGDBA	CDGFCCGRA	CDCDDABCA	PZEAEFB

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
51.	Scelionidae: Aff. *Idris* sp.	[36]	Grimaldi *et al.* 1989
52.	Scelionidae: *Proteroscelio* sp.	[35]	Köningsmann 1978a
53.	Proctotrupidae: *Cryptoserphus pinorus* Brues, Diapriidae: *Ambositra* sp.	[19]	Brues 1940a; Masner 1969; Köningsmann 1978a; Keilbach 1982
54.	Diapriidae: *Galesimorpha* sp.	[15]	Köningsmann 1978a
55.	Scelionidae: *Palaeogyron muesebecki* Masner	[11]	Keilbach 1982
56.	Platygasteridae: *Platygasterites femoralis* Statz, Heloridae: *Helorus festivus* Statz	[8]	Statz 1938; Köningsmann 1982
57.	Mymaridae: *Galoromma bezonnaisensis* Schlüter	[45]	Schlüter 1978
58.	Trichogrammatidae: *Enneagmus pristinus* Yoshimoto, Myrmaridae: *Carpenteriana tumida* Yoshimoto	[35]	Yoshimoto 1975
59.	Eurytomidae: *Decatoma antiqua* Scudder	[23]	Yoshimoto 1975
60.	Eupelmidae: *Propelma rohdendorfi* Trjapitzin, Chalcidae: *Cryptoserphus gracilis* Brues, Perilampidae: *Perilampus* sp.	[19]	Brues 1939; Yoshimoto 1975; Keilbach 1982
61.	Agaonidae: *Tetrapus mayri* Brues, Chalcidae: *Chalcites debilis* Heer	[15,13]	Heer 1856; Brues 1910; Yoshimoto 1975
62.	Mymaridae: *Alaptus psocidivorous* Girault	[11]	Doutt 1973
63.	Pteromalidae: *Pteromalites oeningensis* Heer	[3]	Heer 1865; Yoshimoto 1975
64.	Ibalidae	[39]	Rasnitsyn 1988
65.	Aulacidae: *Mesaulacinus oviformis* Martynov	[60]	Martynov 1925

MOUTHPART CLASS 34: NONTROPHIC
Fig. 130

1.	?Mnesarcheidae	[37]	Skalski 1979b
2.	*Prohepialus incertus* Piton, leaf-mine	[27]	Piton 1940
3.	*Wiseana signata* Walker	[21]	Harris 1984
4.	*Prohepialus* sp.	[18]	Jarzembowski 1980
5.	Sphingidae: "Sphingiden-Raupe"	[6]	Zeuner 1931
6.	Saturniidae: *Attacus fossilis* Cockerell	[15]	Cockerell 1922
7.	Saturniidae: *Aglia tau* Linneaus	[Pleist.]	Koponen & Nuorteva 1973

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
405.	COL	*Amara* sp.	CAABAAAA	CAD	BAABCA	DB	CBGA	CJN	CBCBA	CDGDCBGKA	DCFDDJHCA	EUDDDFA
406.	COL	*Badister** sp.	CAABAABA	CAD	BAABDA	AA	DBBA	CJA	CFDBA	BDHEBCNQA	D CDBABDA	EQCEDDA
407.	COL	*Calosoma inquisitor*	CACBAAAA	CAD	BAABCA	DB	DBCA	CJN	CFDBA	BCSECBGKA	ECFDCJHBA	EQBEEFA
408.	COL	*Calosoma sycophanta**	CAEBABBA	CEA	BAABDA	AA	CABA	CJA	CFDBA	BDHDCCNQA	D GDDHCDA	EQBDDDA
409.	COL	*Carabus auronitens*	CABBAAAA	CAD	DAABCA	DE	DBGA	CBN	CFJBA	CEGDDBGKA	DDFDCLABA	EQCEDFA
410.	COL	*Carabus** sp.	CAEBABBA	CEA	BAABDA	DC	CBEA	C N	CGPBA	CCGECBGPA	DCFCDNACA	EQCEDDA
411.	COL	*Cicindela campestris*	CA BAAAA	CAD	BAABCA	DB	CBDA	CJN	CFDBA	CDGECBGKA	ECFDCJHBA	EQCEDFA
412.	COL	*Cicindela hirticollis**	CAEBABAA	CEA	BAABDA	BE	CBDA	CJA	CGBBA	CDGECBNQA	DDGDLJBDA	EQCEDDA
413.	COL	*Cychrus* sp.	CACBAAAA	CAD	BAABCA	AA	CBCA	CJN	CBLBA	CDGDDBGKA	DCFDCJHBA	E=AEDFA
414.	COL	*Drypta* sp.	CACBAAAA	CAD	BAABCA	AA	CB A	CJN	CCLBA	CDGECEGKA	DCFDDJHBA	EQDEEFA
415.	COL	*Harpalus calignosus*	CACBAAAA	CAD	BAABCA	DB	CBBA	CJN	CBLBA	CDGECBGKA	DDFDDJHBA	E&CDEFA
416.	COL	*Harpalus** sp.	CAEBABBA	CEA	BAABDA	AA	AAAA	CJA	CBDBA	BDHDCBNQA	D GDDHBBA	EQCDDDA
417.	COL	*Loricera pilicornis*	CACBAAAA	CAD	BAACCA	DB	CBCA	CJK	CBCBA	CDGECBGKA	DDFDDJHBA	EQBDDFA
418.	COL	*Loricera** sp.	CAEBABAA	CEA	BAABDA	DB	DBBA	CPE	CFDBA	CCGECBGPA	DCFCDBABA	EQCDBDA
419.	COL	*Megacephala klugi*	CACBAAAA	CAD	BAABCA	B	DBIA	CJN	CFDBA	CCGECBGKA	ECDDDFABA	EQCEDFA
420.	COL	*Nebria brevicollis*	CACBAAAA	CAD	BAACCA	DB	DBGA	CJN	CBCBA	CCGECBGKA	DDFDDJHBA	EQCDDFA
421.	COL	*Nebria** sp.	CAEBAABA	CEA	BAABDA	E	AEIA	CHA	CGPBA	DBGECCGPA	DBDDDHACA	EQCDDDA
422.	COL	*Paussus* sp.	CACBAAAA	GAD	BAABCA	B	DCBA	CJN	CBDBA	BDHEHDNQA	DCFDDJHCA	EGAEDFA
423.	COL	*Pterostichus madidus*	CACBAAAA	CAD	BAACDA	DB	CBGA	CJN	CFLBA	BCGECBGKA	DCFDDJHBA	E&CEDFA
424.	COL	*Scarites** sp.	CAEAABBA	CEA	BAABCA	D	AE A	CPN	CFDBA	DCJECCGAA	DCFCCJHBA	EQCEDDA
425.	COL	*Stomis pumicatus*	CA BAAAA	CAD	BAABCA	DB	CBGA	CJN	CFLBA	CCGEC GKA	DCGCDBCBA	EQDEDFA
426.	COL	*Tetrarcha* sp.	CAABAAAA	CAD	BAABCA	DB	DBMA	CJN	CFDBA	CDGEC GKA	DCFDDJHCA	EQCEEFA
427.	COL	*Trechus quadristriatus*	CACBAAAA	CAD	BAABCA	DB	DBGA	CJN	CFLBA	BDGECBGKA	DCGDDBCBA	EQDEDFA
428.	COL	*Tricondylia aptera*	CACBAAAA	A	BAABCA	B	CBMA	CJN	CFEBA	CDGEHBGKA	ECFDLJHDA	EQCEEFA
429.	COL	*Brychius** sp.	CAEBABBA	MEA	BHCBBA	DE	DBGA	CPE	CJPBB	BCGDJDH A	DCFCJBADA	DACBBDA
430.	COL	*Haliplus** sp.	CAEBABBA	CEA	BHCBBA	DE	DBBA	CJE	CJPBB	BCGDJDH A	DDFCJBADA	DACBBDA
431.	COL	*Peltodytes duodecimpunctatus*	CAABAAAA	CAB	BAABCA	DB	CBGA	CPN	CBDBA	CDGECCGKA	ECFDDBACA	E&CDBFA
432.	COL	*Peltodytes** sp.	CAEBABBA	CEA	BHCBBA	DB	DBGA	CFE	CJPBB	BCGCJDH A	DCFCJBACA	D&CBBDA
433.	COL	*Amphizoa ?insolens*	CACBAAAA	CAD	BAABCA	DB	DBCA	CPN	CDLBA	BDGECCJKA	DCFDDBACA	EQCDCFA
434.	COL	*Pelobia tarda**	CAEBAABA	CEA	BHCBDA	DB	DBCA	ABE	CJBCB	BCFEBBAAA	DCFCBBABA	DQCDBDA
435.	COL	*Hydrocanthus ?iridicolor**	CAEBAABA	BEA	BAABBA	DE	DEBA	CP	CJPBA	BCFDBCAAA	DCECBAACA	DQCBBDA
436.	COL	*Colymbetes sculptilis*	CAABAAAA	CAD	BAABCA	DB	DB A	C	CFBBA	BDGECCGKA	ECFDDHABA	EQCDBFA
437.	COL	*Cybister fimbriolatus**	CAEBABBA	CEA	BHCBBA	DE	EMA	CPE	CJBBB	DCFGCEAAA	DCFEDFABA	DQCBBDA
438.	COL	*Dytiscus circumcinctus*	BACBAAAA	CAD	BAABCA	DB	DBGA	CPN	CBLBA	CDGECBGKA	ECFDDKABA	EQCDBFA
439.	COL	*Dytiscus** sp.	CAEBABAA	CEA	BHCBBA	DE	BEGA	APE	CJBCB	DBFGCEAAA	DDEEDAABA	DQCDBDA
440.	COL	*Hyphydrus aubei**	CAEBABAA	CEA	BHCBFA	BE	AEMA	AQH	CJBCB	BCFDBEAAA	DCECDAABA	DQCBBDA
441.	COL	*Laccophilus testaceus**	CAEBABAA	CEA	BHCBFA	CE	BEGA	AQH	CJBCB	BCJDCEPAA	CCECDAABA	DQCBBDA
442.	COL	*Oreodytes rivalis**	CAEBABAA	CEA	BHCBFA	CE	AEGA	AQH	CJBCB	BCFDCBAAA	CCECDAABA	DQCBBDA
443.	COL	*Dineutes discolor*	BACBAAAA	PAE	BAABCA	DB	DBGA	CEM	CFABA	CDKECCAKA	ECFDDBACA	EQCDBFA
444.	COL	*Dineutes** sp.	CAEBABAA	CEA	BHCBBA	DE	DEGA	APE	CJBCB	CCGECBGKA	DDEDDAABA	DQCDBDA
445.	COL	*Gyrinus substriatus*	CACBAAAA	PAE	BAABCA	DB	DBGA	CPB	CFABA	BCGECCGKA	DCFDDBACA	EQCDBFA
446.	COL	*Orechtochilus villosus**	CAEBAABA	CEA	BHCBBA	DE	DEBA	AAE	CJBCB	BCGECBGKA	DDEDDAABA	DQCDBDA
447.	COL	*Ochtebius impressus**	CAEBABBA	CEA	BAABDA	DC	CBFA	C E	CFKBA	BDGDBCDKA	CDFCDHADA	E*CCCDA
448.	COL	*Cephaloplectus mus*	BAAAAAAC	GAA	CAABCA	DB	DBGA	CFE	CBDBA	BDGECCHJA	DCGDDFDCA	ESAEFFA
449.	COL	*Anisotoma blanchardi**	CAEBABBA	CEA	BAABDA	DB	CBBA	CHB	CFNBA	CCGDBCHIA	DCGDBOFCA	ENAEEDA
450.	COL	*Cainosternum imbricatum*	BACBAAAA	GAC	BAABCA	DB	DBGA	CCC	CCNBA	BDGDCCHKA	EBFDDBACA	ELBEEFA
451.	COL	*Speophyes lucidulus**	CAECABBA	PAA	BAACBA	AE	DBGA	JE	CJEBA	BDGDBCBNA	DBFCBBACA	DLCBEDA
452.	COL	*Leptinus testaceus*	CAABAAAC	GAA	CAABCA	AA	DBBA	CPE	CAAAA	BDGECCHJA	DCFDBBACA	ETBEFFA
453.	COL	*Platypsyllus* sp.	CAACAAAC	GAA	CAABCA	AA	DBBA	CPE	CAAAA	CCGECCHJA	DBFDBAADA	ETAEFFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
454.	COL	_Scydmaenus tarsatus_*	CAEBABBA	PEA	BAABDA	AA	DBGA	CJE	CFBBA	BCGDBCHMA	DCFCBFACA	E=BDEDA
455.	COL	_Necrophorous_ sp.	CACBAAAA	GAD	BAABFA	DC	DBCA	CPE	CFDBA	BDGECBHKA	DCFDDBABA	EWCDDFA
456.	COL	_Silpha americana_	CACBAAAA	GAD	BAABFA	AA	DBCA	CCE	CFDBA	BDGECBHKA	DCFDDBBBA	EWCDDFA
457.	COL	_Silpha noveboracensis_*	CAECABBA	FEA	BAABFA	DB	BBBA	CCE	CFDBA	BCGECCHKA	DDFCDBACA	EWCDDDA
458.	COL	_Thanatophilus_* sp.	CAECABBA	FEA	BAABFA	DB	CBCA	CAE	CFDBA	BCGECBHKA	CDFCDCADA	EWCDDDA
459.	COL	_Agaricochara laevicollis_	CABBAAAC	GAD	CAABCA	DB	DBCA	CA	CBJBA	CEGEDCHJA	DCDCBFACA	EOBDEFA
460.	COL	_Brachida exigua_	CABBAAAA	GAD	BAABCA	AA	DBGA	CA	CBJBA	BEGEDCHJA	DCFCBBACA	EOCDEFA
461.	COL	_Brachychara ?crassa_	CABBAAAA	GAD	CAABCA	DB	CBCA	CA	CBJBA	CEGEDBHJA	DCDCBFACA	EOBDEFA
462.	COL	_Creophilus villosus_	CABBAAAA	GAB	BAABFA	DC	DBGA	CFA	CFLBA	CEGECCHJA	DCFDDBACA	EUCEDFA
463.	COL	_Dianous coerulescens_	CABBAAAA	GAB	BAABCA		DBGA	CCA	CFIBA	CEGEECHJA	DCGCCFKCA	EQCDCFA
464.	COL	_Eumicrota corruscula_	CABBAAAA	GAD	BAABCA	DB	CBCA	CCA	CBJBA	BEGEDCHJA	DCFCBBACA	EOCDEFA
465.	COL	_Gyrophaena affinis_	CABBAAAA	GAD	BAABCA	DB	CBCA	CA	CBJBA	CEGEDBHKA	DCFCBBACA	EOBDEFA
466.	COL	_Loeblius nepalensis_	DAABABAA	GAA	BAABCA	AA	CBGA	CCA	CFBBA	CDGEDCHMA	DCGDDCCCA	EQBDDFA
467.	COL	_Megaquedius explanatus_	CACBAAAA	GAD	BAABCA	DB	DBCA	CCA	CFDBA	BDGCCCHKA	DDGBDCCCA	ETBDFFA
468.	COL	_Pachorhopala jeaneli_	CACBAAAA	GAD	BAAB A	AA	CBMA	CCA	CBBBA	CEGECBHKA	DDDDBFACA	EQDDAFA
469.	COL	_Phanerota insigniventris_	CABBAAAA	GAB	BAABCA	DB	DBCA	CCA	CBJBA	CEGEDCHKA	DCFCBFACA	EOCDEFA
470.	COL	_Philonthus decorus_	CABBAAAA	GAD	BAABCA	DB	DBCA	CCN	CFDBA	BEGECBHKA	DDDDDBACA	EQCDDFA
471.	COL	_Pseudolignota affinis_	CABBAAAA	GAD	BAABCA	DB	DBCA	CCN	CBJBA	CEGED HJA	DCDCBFACA	EOCDEFA
472.	COL	_Staphylinus olens_	CABBAAAA	GAD	BAABCA	AA	DBCA	CCN	CFDBA	CEGECBHKA	DDGDDFFCA	EQCDEFA
473.	COL	_Staphylinus_* sp.	CAECABBA	CEA	BAABDA	AE	AEGA	CAE	CGBBA	CCHDCCNQA	DDFCBFACA	EQCDEDA
474.	COL	_Stenus bipunctatus_	CABBAAAA	GAB	BAABCA	AA	DBBA	CCA	CFIBA	CEGECEHJA	BDGDCNECF	EQCDEFA
475.	COL	_Stenus biguttatus_*	CAECABAA	CEA	BAABDA	AE	AEGA	CAE	CGIBA	BCHDBENQA	DBFCBBACA	EQCDEDA
476.	COL	_Sternotropa brevicornis_	CABBAAAA	GAD	CAABCA	DB	DBCA	CCA	CBJBA	CEGEDCHJA	DCDCBFACA	EODDEFA
477.	COL	_Thinopinus pictus_*	CAECABAA	CEA	BAABDA	AE	AEMA	CAE	CGBBA	CCHDCCNQA	DDFCBBADA	EUCDEDA
478.	COL	_Rhinoscepsis bistriatus_	CABBAAAA	HAD	BAABCA	AE	CBMA	CCA	CFDBA	CEKEDCAKA	DDECCAACA	ELDEDFA
479.	COL	_Trichonyx sulcicollis_*	CAECABBA	OAA	BAABDA	AE	DBBA	CAE	CFDBA	CCHDBCNQA	CCECBAACA	EQCDGDA
480.	COL	_Aculomicrus pusio_	CCCBAAAA	GAD	BEABCA	DB	BBFC	CPI	CQIBE	BCGECBFBE	CCDDHPACB	KVCBDFB
481.	COL	_Berosus_ sp.	BAABAAAA	HAD	BAABCA	CB	DBEA	CPE	CFDBA	CCFECEAAA	DCFCDOABA	EUCDBFA
482.	COL	_Hydrobius_* sp.	CAEAABBA	CEA	BAABDA	DE	DEMA	CBE	CFDBA	CCJDBCBAA	DDFCBFACA	EQCDBDA
483.	COL	_Hydrochus squamifer_*	CAEBABBA	CEA	BAABBA	CE	AAAA	C A	CFDBA	CCFDBDAAA	CCECBAADA	EQCDBDA
484.	COL	_Hydrophilus caraboides_*	CAEAABBA	EEA	BAABDA	DE	DEMA	CBE	CFDBA	DCJDBBBAA	CDFCBFACA	EQCDBDA
485.	COL	_Hydrophilus obtusatus_	CAABAAAA	HAD	BAABCA	DB	DBGA	CBE	CFDBA	CDGECEHKA	DCGCDBCBA	EUCDBFA
486.	COL	_Hydrous triangulatus_*	CAEAABBA	CEA	BAACDA	DE	DEBA	CBE	CFIBA	DCJDCBBAA	DDFCDFACA	EQCDBDA
487.	COL	_Philhydrus testaceus_*	CAEAABBA	CEA	BAACDA	DE	DEMA	CBE	CFDBA	CCJDBCBAA	DDFCDFACA	EQCDBDA
488.	COL	_Spercheus emarginatus_*	CAEBABBA	CEA	BAABBA	CE	DBGA	CBC	CFFBA	BCGDCCFKA	DCFCDFADA	DQCDBDA
489.	COL	_Sphaeridium scarabaeoides_	CABBAAAA	HAD	BAABCA	DB	DBBA	CPE	CFBBA	BDGEDCHPA	DDFDCBACA	EACDDFA
490.	COL	_Sphaeridium_* sp.	CAEBABBA	CEA	BAABDA	CE	DEEA	CBE	CFBBA	CCJDBCBAA	DDFCDAACA	BQCBDDA
491.	COL	_Tropisternus glaber_	CACBAAAA	GAB	BAABCA	DE	DBBA	C E	CBDBA	CDGECEHJA	DDGDDFKCA	E&CDBFA
492.	COL	_Georyssus laevicollis_	CACCAAAA	GAD	BAABCA	CB	DBCA	C	C BA	CDGECCBKA	CCFECCACA	E CFA
493.	COL	_Sphaerites glabratus_	CACBAABA	GAD	BAABCA	DB	CBBA	C	CFDBA	BDGECCHKA	DCFEDBACA	EIDBEFA
494.	COL	_Hister obtusatus_	CACAAABA	GAD	BAABCA	DB	DBBA	C	CFDBA	BDGECBHIA	DCGDDACCA	EPCDDFA
495.	COL	_Hololepta_* sp.	CAEAABBA	CAA	BAABDA	AA	AAAA	C	CFPBA	CCJDCCBAA	CDFCBAACA	EQCDDDA
496.	COL	_Eucinetus meridionalis_	CACBAAAA	GAB	BAABCA	DB	DBBA	CBA	CBLBA	CDSECCHKA	DDFDDLACA	E*CCDFA
497.	COL	_Eucinetus morio_*	CAEAABBA	CEA	BAACDA	AE	DBGA	CCE	CBCBA	BCGCCCBDA	DCGCDBBDA	ELCEDDA
498.	COL	_Jentozkus plaumanni_	CCBBAAAC	GAD	CCEBFA	BB	BBHI	BBA	AAAAE	CCGECBCDF	DCFDDAACI	B DBDFA
499.	COL	_Tohklezkus ponticus_	CCBBAAAC	GAA	BCEBFA	BB	BBHI	BBA	AAAAE	CCGECBCDF	DCFDDAACI	BZCBDFA
500.	COL	_Clambus punctulatum_	CABBAAAA	GAD	BAABCA	DB	CBBA	CCA	CFDBA	CDGECCGKA	DCFDDBACA	EUCDDFA
501.	COL	_Elodes marginata_*	CAEBABBA	CEA	BAABDA	AE	DBGA	CFG	CBLBA	BCGDCBHKA	DCECDAACA	E*CCBDA
502.	COL	_Prionocyphon discoideus_*	CAEBABBA	BEA	BAABDA	AE	CBCA	CFG	CFLBA	BCGECBHKA	DCECDAACA	E*CCBDA

	order	taxon	mouthpart morphology data									dietary
			I	II	III	IV	V	VI	VII	VIII	IX	data
503.	COL	*Scirtes tibialis*.	CABBAAAA	CCD	BAABCA	DB	DBEA	CBC	CBBBA	BDGEDBHJA	DCFD FACA	QZEADFA
504.	COL	*Dascillus cervinus**	CAECABBA	CAD	CAACDA	CE	DBGA	CFG	CBEBA	BDGDCCPMA	CDECDAACA	EVCDGDA
505.	COL	*Trichentoma childreni**. . . .	CAEAABBA	CAA	CAABDA	DE	DBGA	CB	CBDBA	BDGDBCBIA	CCFCDCADA	E*CDDDA
506.	COL	*Sandalus niger*.	CBCBAAAA	EAD	BAABCA	CB	AAAA	CBE	CBDBA	CCGECBFRA	DCFDDBABA	ETBDGFA
507.	COL	*Lucanus cervus*.	CABBAAAA	IAD	BAABCA	AE	AEAA	CBE	CFDBA	CCGECBAAA	DCDDDLACA	EIBBDFC
508.	COL	*Lucanus cervus**	CAECABBA	CAA	CAABDA	DB	CBGA	CRE	CFDBA	BCGDBCPKA	DDFCBAADA	EZDBDDA
509.	COL	*Pseudolucanus capreolus* . . .	CACBAAAA	IAD	BAABCA	AE	CBBA	CBE	CFDBA	CCGECBHBA	DCDDDLABA	EGBBDFA
510.	COL	*Sinodendron cylindricum**. . .	CAECABBA	CAA	CAABDA	DB	CBBA	CRE	CFDBA	CCGDCCPKA	DCECBAADA	EZCBDDA
511.	COL	*Passalus cornutus*	CAACAAAA	GAD	BAABCA	DE	DBCA	CPE	CQDBA	CEGECBPKA	DCFCDBACA	EZCDDFA
512.	COL	*Passalus cornutus**.	CAECABBA	OAA	CAACDA	DB	CBGA	CRI	CFCBA	BDGCCDPKA	DCFCBBADA	EZCDDDA
513.	COL	*Popilius disjunctus**.	CAEBABBA	OAA	CAABCA	DB	DBGA	CRI	CDEBA	BDGDCDPKA	DCFCDHADA	EZCDDDA
514.	COL	*Trox scaber**.	CAECABBA	OAA	CAACDA	DB	CBGA	CRC	CBNBA	BCGDCCPKA	DCFDDBADA	EWCDDDA
515.	COL	*Geotrupes stercorarius*. . . .	CACBAAAA	JAD	BAABCA	D	CBMA	CPE	CMLBA	CEGECBHJA	CCDDDCACA	IXCEGFA
516.	COL	*Geotrupes splendidus**	CAEAABBA	OAA	CAACDA	CE	DBGA	CRI	CBEBA	BCGEBCPKA	DCECBAACA	EXCEGDA
517.	COL	*Diphyllostoma linsleyi*. . . .	CBCBAAAA	HAB	BAABCA	CB	AAAA	CPE	CBBBA	CCGECBBKA	DCEDDAACA	E DDFC
518.	COL	*Amphimallon majalis*	CABBAAAC	JAD	BAACCA	DE	DBGA	CBC	CBEBA	BCGDDCLKA	DCFCDDACA	EQCEEFA
519.	COL	*Amphimallon majalis**.	CAEAABBA	CAA	CAACDA	DB	DBBA	CRI	CFEBA	CDGDCCJKA	DCFCDHACA	EJBDGDA
520.	COL	*Anastrategus splendens** . . .	CAEAABBA	CCA	CAACDA	DB	CBGA	CRI	CFCBA	BDGDCCPKA	DCFCDHACA	EZCDDDA
521.	COL	*Aserica castanea**	CAEAABBA	CCA	CAACDA	DC	CBGA	CRI	CFCBA	BDGDCCPKA	DCFCDHACA	EJBDDDA
522.	COL	*Cetonia aurata*.	CABBAAAC	JAD	CAAB A	CB	BJA	CPE	CMIBA	CDGECBHJA	DCFDDLACA	EDDCEFA
523.	COL	*Melolontha hippocastani**. . .	CAECABBA	CAA	CAACDA	DB	CBGA	CRI	CFLBA	BDGECBPKA	CCFCDHACA	EJBDGDA
524.	COL	*Melolontha vulgaris*	CA AAAC	JAD	CAACBA	DB	DBCA	CPI	CBNBA	BDGEDBLRA	DCFDCLA A	EEDDEFA
525.	COL	*Neodon pecuarius*.	CABBAAAC	JAD	CAAB A	CB	CBJA	CPE	CBIBA	CDGEDBPMA	DCFDCFACA	EECDEFA
526.	COL	*Oryctes grypus*.	CABBAAAC	JAD	CAACCA	DD	CBBA	CPE	CBLBA	BDJECBLAA	DCFDDLACA	EZCEDFA
527.	COL	*Oryctes nasicornis**	CAEAABBA	CAA	CAACCA	DB	CBGA	CRI	CBDBA	BDGECCPKA	DDECDAACA	EACDEDA
528.	COL	*Phyllophaga rugosa**	CAEAABBA	CAA	CAACCA	DB	CBGA	CRI	CBJBA	CDHECBNQA	DDFCDBACA	EJBDGDA
529.	COL	*Pimelopsis porcellus*.	CABBAAAC	JAD	CAABCA	DD	CBMA	CPE	CMLBA	CDJEDBLAA	DCFDCBABA	EEBDEFA
530.	COL	*Popillia japonica*	CACBAAAC	JAD	BAABCA	DD	DBBA	CPB	CBNBA	CDJECCLAA	DCFCDBACA	EACDEFA
531.	COL	*Popillia japonica**.	CAEAABBA	CAA	CAACDA	DB	CBGA	CRI	CMJBA	CDHECBNQA	DDECDAADA	EJBDGDA
532.	COL	*Scarabaeus sacer*.	CACBAAAC	JAD	CAABCA	DB	CBMA	CPE	CMLBA	CDGECBFKA	DCFDFLABA	IXCEDFA
533.	COL	*Byrrhus americana*	CACBAAAA	GAD	CAABCA	AA	CBCA	CJE	CBDBA	CDGECBHJA	DDDDDHACA	EEBDEFA
534.	COL	*Byrrhus fasciatus**.	CAECABBA	OEA	CAABDA	DB	DBGA	CB	CBLBA	BDGDCDPKA	DDDCDBADA	EEBDEDA
535.	COL	*Chalcophora virginiensis** . .	CAECAABC	OAA	BAABDA	DB	DBGA	CRN	CBDBA	BCHCJDQHA	DCBAAHAAA	RKADEDA
536.	COL	*Chrysobothris femorata** . . .	CAECAABC	OAA	BAABDA	DB	CBGA	CRN	CBDBA	BCHCJDQHA	CBAAHAAA	RKCDEDA
537.	COL	*Ptilodactyla serricollis** . .	CAEAABBA	OEA	BAABDA	DB	DBJA	CBE	CBHBA	BDGEBCPMA	DDFCBBACA	E*CCBDA
538.	COL	*Chelonarium ornatum*	CACBAAAA	CAB	CAABCA	DB	DBBA	CJE	CFBBA	BEGEDCGBA	CDDDDGACA	EEDDEFA
539.	COL	*Heterocerus paralleleus* . . .	CAACAAAA	FAD	BAABCA	DB	CBGA	CJE	CFBBA	DEGDCCHKA	DDFDDLABA	ELCDGFA
540.	COL	*Limnius troglodytes**.	CAECABBA	OCA	BAABDA	DB	DBGA	CPC	CBHBA	CCGDCCIMA	DCFBJBADA	EUCEGDA
541.	COL	*Lutrochus arizonicus*.	CBCCAAAA	FAD	BAABCA	DB	CBGA	CJE	CFLBA	BEGEDCHJA	CCFDCHACA	E DBFC
542.	COL	*Helichus fastigatus*	CACBAAAA	EAD	CAABCA	DE	DBGA	CJE	CFDBA	CDHEECQHA	DCFDNHACA	EACDBFA
543.	COL	*Helichus** sp.	CAEAABBC	OCA	BAABDA	DB	DBJA	CBE	CFHBA	CDGECCHMA	DBFCDBADA	EJCDBDA
544.	COL	*Riolus** sp.	CAEBABBA	OCA	BAABDA	DC	DBBA	CPC	CBHBA	CCGECCJMA	DCFCJHADA	EACDDDA
545.	COL	*Stenelmis crenata**.	CAEAABBC	OEA	BAABDA	DB	DBGA	CBE	CBHBA	BDGECCPMA	DBFCDBADA	E*CDADA
546.	COL	*Psephenus lecontei*.	BACBAAAC	CAB	CAABCA	DB	DBGA	CJE	C BA	BEGEEBBBA	DCFDDBACA	QZEACFA
547.	COL	*Artematopus discoidalis**. . .	CAEBABBA	OCA	BAABCA	CE	BBGA	CGK	CFLBA	BCGEBCGMA	DCFCDJHCA	EQCDDDA
548.	COL	*Agriotes** sp.	CAEAABBA	OAA	BAABDA	DE	CDDA	CBA	CFHBA	CCGEBCHCA	CCFCBNADA	EJCDGDA
549.	COL	*Alaus oculatus*.	CABBAAAA	FAD	BAABCA	E	DBGA	CJE	CFBBA	CDGEDBHJA	CDFDCLACA	EEDFEDA
550.	COL	*Alaus oculatus**	CBECAABA	OAA	BAABDA	DE	CDAA	CBA	CFBBA	CDGECCGJA	CCFCDFADA	EZCDEDA
551.	COL	*Horistonotus uhlerii**	DAEAABAA	OAA	BAABDA	CB	CDCA	CBA	C LBA	DBJEBCHAA	BBECBAACA	EACDGDA
552.	COL	*Neotrichophorous carolinensis*	CABCAAAA	FAB	BAABCA	AE	DBGA	CJE	CFBBA	CDGEEB A	DDBDFLACA	QZEADFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
553.	COL	_Parallelostethus attenuatus_*	CAEAABBA	MAA	BAABDA	DE	CDMA	CBA	CFDBA	CDJEBCGAA	CDFCBBADA	Q%EADDA
554.	COL	_Cebrio bicolor_	CACBAAAA	FAB	BAABCA	CE	DBGA	CJE	CFBBA	BDGECEHJA	CDFDDLABA	EUCDEFA
555.	COL	_Cebrio antenuatus_*	CAECABBA	AAA	CAABDA	CE	CDMA	CBA	CFBBA	CDGECCGJA	CDFCDLACA	EJDDGDA
556.	COL	_Oestodes tenuicollis_*	CAECABBA	OAA	BAABDA	CE	CDDA	CBA	CBDBA	CCJEBDGAA	CCFCDFADA	EJDDGDA
557.	COL	_Throscus dermestoides_	CACBAAAA	FAE	CAABCA	DE	DBGA	CJE	CFDBA	BDGECBHJA	DCFDCLACA	EDCDEFA
558.	COL	_Eucnemis capucina_	CACCAAAA	FAD	CAABCA	AE	DBGA	CJE	BBDBA	BDGEDCHCA	DDFDCFACA	EZDBDFA
559.	COL	_Melasis rufipennis_*	CAEBAABA	AAA	BAABDA	AA	AAAA	DAA	C IBA	AAFDIAAAA	DCAAAAAAA	RZCBEDA
560.	COL	_Rhinorhipus tamboriensis_	CBCCAAAA	CAD	BAABCA	BB	CBJA	CFC	CFBBA	CEGEDBHJA	CCFDCLACA	EA DGFC
561.	COL	_Brachypsectra fulva_*	CAEAABBA	GAA	BHCBDA	CE	CDIA	CBA	CJBCB	CCJEDDPAA	CCDCDDACA	EQCDDDA
562.	COL	_Calochromis tarsalis_*	BAEBABBA	MCA	BHCBBA	AA	AAAA	CBA	CPABB	CBJDJDPAA	DBECJAADA	DQCBDFA
563.	COL	_Calopteron reticulatum_*	CAEBABBA	MAA	BHCBBA	AA	AAAA	CBA	CPABB	BBGEBDPAA	DCEDBAACA	DQCBDDA
564.	COL	_Eros aurora_*	CAEBABBA	MAA	BHCBBA	AA	AAAA	ABA	CPABB	BBJDJDPAA	DCECJAADA	DQCBEFA
565.	COL	_Lycus_ sp.	CCCCAAAC	CAB	CAABCA	AE	CB A	CJE	CFBBA	CDGEDBHBA	BCFDDFACA	EQCDEFA
566.	COL	_Drilius concolor_*	CAEAABBA	OAA	BHCBDA	CE	CDEA	ABA	CJBCB	BCJEJDPAA	BDECDAACA	D=BBDDA
567.	COL	_Phenogodes laticollis_*	CAECABAA	OCA	BHCBBA	AA	ADAA	ABA	CJBCB	CCJECCGAA	CDFCDFADA	DQCBDDA
568.	COL	_Phenogodes_ sp.	CACAAAAA	EAB	BAABCA	DE	DBGA	CJE	CGBBA	BDGEDCHJA	CCFDDHACA	EQBDDFA
569.	COL	_Lampyris noctiluca_*	CAECABBC	OCA	BHCBBA	DE	ADEA	ABA	CJBCB	CCJEJDGAA	BCECBAADA	D=CBEDA
570.	COL	_Lamprophorus tenebrosus_*	CAEBABBC	CCA	BHCBDA	DE	AAAA	ABA	CJKCB	CCJCJDGAA	CCECBAADA	D=CBDDA
571.	COL	_Luciola dubia_*	CAECABBC	OCA	BHCBDA	DE	AAAA	ABA	CJKCB	DCJEBDGAA	CCECDAADA	D=CBDDA
572.	COL	_Photinus pyralis_*	CAECABBC	OCA	BHCBDA	DE	ADDA	ABA	CJKCB	CCJDBCGAA	CCFCBBADA	D=CBDDA
573.	COL	_Photuris pennsylvanica_*	CAEBABBC	OCA	BHCCDA	CE	CDDA	ABA	CJKCB	CCGEBDGKA	CCECBAADA	D=CBDDA
574.	COL	_Cantharis andersoni_	CACBAAAC	CAD	CAABCA	DB	DBGA	CRA	CFBBA	CDGEDBHKA	DCFDCIACA	EDCDEFA
575.	COL	_Cantharis rustica_*	CAECABBA	OCA	BHCBDA	DE	AAAA	ABA	CJKCB	CCJEBCGAA	CCECBAADA	DQCDEDA
576.	COL	_Chauliognathus pennsylvanicus_	CABAAAA	CAD	BAABCA	DB	DBCA	CRA	CFBBA	CDJEDBJAA	CCFDCFACA	EHBEEFA
577.	COL	_Derodontus maculatus_	CABBAAAC	GCD	CAABCA	DE	CBGA	CBI	COBBA	BEGECCHJA	DCGDDQBCA	EOCDEFA
578.	COL	_Nosodendron californicum_	CACCAAAA	GAD	BAABCA	DB	DBEA	C	CFBBA	BDGECCHKA	DCFDCHACA	EIBBEFA
579.	COL	_Nosodendron unicolor_*	CAEAABBA	OEA	BAABDA	DD	DEEA	CBN	CBJBA	BCGDCCHKA	DDGCDHCDA	EMCDEDA
580.	COL	_Anthrenus fasciatus_*	CAEBABBA	OEA	CAABDA	DB	DBGA	CBC	CBDBA	BCGDBDHKA	DDDCJHADA	E$CDFDA
581.	COL	_Dermestes lardarius_	CABBAABC	GBD	CAABCA	DB	DBCA	CBN	CBHBA	BDGECCHKA	CCGDDFHCA	EWCDDFA
582.	COL	_Dermestes vulpinus_*	CAECABBA	OEA	CAABDA	DB	DBGA	CBI	CBLBA	CEGDBDHJA	CDCCBACDA	EWCDDDA
583.	COL	_Saphophagus minutus_*	CAEBABAA	OAA	BAABDA	CE	CBBA	CCE	CBEBA	CCHDCCQHA	DCDCDOACA	E DDDA
584.	COL	_Apatides fortis_	CABCAABC	GAD	CAABCA	DB	DBNA	CBJ	CFBBA	CDGECBHJA	DDCDDACBA	RKCDEFA
585.	COL	_Apatides fortis_*	DAEAABBC	OCA	BAABDA	DB	DBGA	CBI	CNBBA	BCGCCCHDA	DDFCDOACA	RKBDEDA
586.	COL	_Lyctus linearis_	CAABAAAA	GAD	BAABCA	DB	DBGA	CBI	CFDBA	BDGECBHJA	DCGDDLKCA	RKCDEFA
587.	COL	_Scobicia declivis_*	CAEAABBC	OCA	BAABDA	DB	DBGA	CBI	CNBBA	CCGCJDHDA	DDFCDHADA	RKCDEDA
588.	COL	_Anobium striatum_*	CAECABBA	MCA	CAABDA	DB	CBGA	CBI	CNDBA	CDJDBDHAA	CDECBHADA	RKCDEDA
589.	COL	_Trichodesma klagesi_*	CAECABBA	MCA	CAABDA	AE	CBGA	CBN	CBDBA	CCGDBDPKA	CDECBAADA	RZDDDDA
590.	COL	_Oligomerus brunneus_	CABBAABC	CAD	CAABCA	DD	CBGA	C	CFBBA	BDGECBHJA	DCFDDOACA	EBCDDFA
591.	COL	_Oligomerus fur_*	CAEAABBA	MAA	CAABDA	DB	DBGA	CBA	CFLBA	CDGDBDPPA	CDEBJAADA	RZDDDDA
592.	COL	_Hylecoetus lugubris_	CABBAAAA	FAD	CAABCA	AA	DBGA	CBE	CBDBA	BCGEDCHRA	CDFDDBACA	EOBDEFB
593.	COL	_Calitys scabra_*	CAECABBA	OEA	BAABDA	DB	DBGA	CBE	CBDBA	BCHDBCNQA	CDECBAADA	EQCDEDA
594.	COL	_Promanus_* sp.	CAEBABBA	OCA	BAABDA	DB	DBBA	C	CBDBA	BCHDCDNQA	CDECDAADA	EQCDADA
595.	COL	_Tenebroides nanus_*	CAECABBA	OEA	BAABDA	DB	DBGA	CBE	CBLBA	CCHDBCNQA	CDECBAADA	EQCDDDA
596.	COL	_Temnochila viriscens_*	CAEBABBA	OEA	BAABDA	DB	DBGA	CBI	CBDBA	CCHDBCNQA	BDFCDFACA	EQCDEDA
597.	COL	_Callimeris arcufer_*	CAEBABBA	OEA	BAABDA	DB	DBGA	CBG	CBDBA	BCHDCCNQA	CDFCDFACA	EQCDEDA
598.	COL	_Enoclarus lecontei_*	CAEBABBA	OEA	BAABDA	DE	DBGA	CBE	CBBBA	BCHDBCNQA	DCECBAACA	EQCDEDA
599.	COL	_Necrobia rufipes_*	CAEBABBA	OEA	BAABDA	DB	CBBA	CB	CBDBA	BCHDBCNQA	CCFCBBACA	EWCDFDA
600.	COL	_Trichodes ornatus_	CACBAAAC	GAD	CAABCA	DE	CBCA	CBE	CFDBA	BDGECCHJA	CCFDCHACA	EQCDEFA
601.	COL	_Dasytes coeruleus_*	CAECABBA	OEA	BAABDA	DB	DBGA	CBI	CBHBA	BCGDCDPKA	DDFCDFADA	EWCDDDA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
602.	COL	*Malachius bipustulatus*.	CABBAAAA	FAD	CAABCA	DB	CBGA	CC	CBDBA	BEGECCHKA	DDFDDHACA	EHBCEFA
603.	COL	*Sphindus dubius*	CACBAAAA	HAD	CAABCA	CB	DBGA	CBE	CFDBA	BDGECCHJA	DCFDDHACA	ELBEDFA
604.	COL	*Glischrochilus obtusatus**	BAEBABBA	OEA	BAABDA	DE	DBBA	CCN	CBLBA	BCHDCCNQA	DCFBDHADA	EVAEEDA
605.	COL	*Prometobia sexmaculata**	BAECABBA	OEA	BAABDA	DE	DBGA	CCN	CBCBA	CCHDCCNQA	BDFBDBADA	EVAEEDA
606.	COL	*Rhizophagus picipes*	CABBAAAA	HAD	BAABCA	AA	DBGA	CBE	CBDBA	CEGEDCHJA	DDDDCCACA	EQDDEFA
607.	COL	*Boganium armstrongi*	CABBAAAA	DAD	BAACCA	CB	BBBA	CBE	CBEBA	BCGECCPMA	CCFDCBACA	EMCCDFB
608.	COL	*Rhophalobrachium clavipes**.	BAECAAAA	OEA	BAACCA	DE	BBBA	CCE	CBLBA	BDHDCCNQA	CCFCDHAEA	EZCEDDC
609.	COL	*Helota gemmata**	CAECABAA	CEA	BAABDA	CE	CEBA	CCI	BFDBA	BDHDCCHJA	DCFCDBICA	EICBEDA
610.	COL	*Cucujus clavipes*.	CACBAAAA	FAD	BAABCA	CE	DBGA	CBE	CFDBA	BDGEDCHJA	DCDDCHACA	EBCDEFA
611.	COL	*Cucujus clavipes**	BAECABBA	CEA	BAABDA	DE	DBGA	CCI	CBLBA	BCHDCCNQA	DDFCDBADA	EQCDEDA
612.	COL	*Oryzaephilus surinamensis**.	CAEBABAA	CDA	BAABDA	DE	DBBA	CDI	CBKBA	CCHDCCNQA	CCFCDNADA	EBCDDDA
613.	COL	*Telephanus ?pallidus**	CAECABBA	CEA	BAABDA	DE	BGA	CCI	CBCBA	BCHDCCNQA	CDFCDBADA	EUCEDDA
614.	COL	*Cavognatha pullivora*.	CBCBAAAA	GAB	BAACCA	CB	BBGA	CBE	CBLBA	BDGECCHMA	BCFDCBACA	EMCDEFC
615.	COL	*Antherophagus ochraceus**.	CAEBABAA	CEA	BAABDA	DE	DBGA	CDB	CBKBA	CCHDCDNQA	CDFBJBADA	EUADDDA
616.	COL	*Cryptophagus saginatus**	CAECABBA	OEA	BAABDA	DE	DBGA	CDB	CBKBA	CCHDCCNQA	DCFBJBADA	EUBDDFA
617.	COL	*Propalticus simplex**.	CAECABAA	OEA	BAABDA	AA	BBGA	CCB	CBLBA	CCHDBCNQA	CCFCDBADA	ELCDEDA
618.	COL	*Lamingtonium binnaburrense*.	CBBBAAAA	GAD	BAACCA	DB	BBBA	CBE	CDLBA	BCGECCHKA	BCFDCBACA	E EFC
619.	COL	*Hydnobioides pubescens*.	CBBCAAAA	DAD	BAACCA	CB	BBCA	CBE	CBEBA	CCGEDCHMA	CCFDCBAEA	EMCCDFC
620.	COL	*Languria angustata**	CAEBABBA	OCA	BAABDA	DE	DBGA	CDB	CBEBA	CCHDBDNQA	DCFCBBADA	RKBDEDA
621.	COL	*Megalodacne grandipennis*.	CACBAAAC	GAD	BAABCA	DE	DDJA	CRI	CFDBA	CDGEDCHJA	DCGDCBKCA	ELCDAFA
622.	COL	*Tritoma unicolor**	CAECABBA	MEA	CAABDA	DE	CBGA	CDB	CBDBA	CDHDBCNQA	DCECJAADA	ELCDADA
623.	COL	*Phalacrus grossus*	CAAAAAAA	HAD	CAABCA	AA	DBGA	CBE	CFDBA	BDGECBHRA	DCFDDHABA	ECBDEFA
624.	COL	*Aculagnathus mirabilis*.	CBBAAABC	GAD	BBEBFA	DE	BBHI	BOL	BKGDF	CEGEHBPDF	CDFDPPACI	BNBBEFA
625.	COL	*Axiocerylon cavicolle*	CBBAAABC	HAD	CBFBFA	DE	CBHI	BOL	BKGDF	BDGECBDDF	CCFDPPACA	BNBBEDA
626.	COL	*Cautomus sugerens*	CCBAAABC	GAD	BBFBFA	DE	EBHI	BOL	BKGDF	BEGEHBDDF	DDDDPPACI	BNBBDFA
627.	COL	*Cerylcautomus floridensis*	CBBAAABC	HAD	BBFBFA	CE	CBHI	BOL	BKGDF	BDGEHBDDF	CCFDPPACI	BNBBEFA
628.	COL	*Cerylon fagi*.	CA BAAAC	GAD	CAABCA	CE	CBGA	CBN	C KBA	BEGEHCJKA	DDFDPHADA	EQCDEFA
629.	COL	*Lapecautomus dybasi*	CBBAAABC	HAD	BBFBFA	DE	CBHI	BOL	BKGDF	CEGEHBDDF	CDFDPPACI	BNBBEFA
630.	COL	*Neoglyptoides jamaciensis*	CA BAAAC	GAD	BAABCA	DE	CBCA	C J	C KBA	CDGEHBPSA	CDFDPCACA	EQCDEFA
631.	COL	*Philothermus bicavus**	CCEBABBA	MEA	BBEBDA	DB	CBHI	BKB	BKGDF	BEKDBBADF	DDFCBBABI	BQCBEDA
632.	COL	*Arthrolips?** sp.	CAEAABBC	OEA	BAABDA	CE	AAAA	CDB	CBEBA	GBHCJDNQA	DCFCJBADA	RKCDEDA
633.	COL	*Hoplicnema sallaei*.	CBCBABBC	GAD	FBEBCB	AE	CAGI	CDE	BQDDF	CEGEHCJDF	CCFDPBBDI	AMCCEFA
634.	COL	*Discoloma cassideum**.	CAEBABAA	CEA	BAABDA	DB	CBBA	CCE	CFEBA	CCGDBCPKA	DCFCBBADA	EQADEDA
635.	COL	*Anatis quindecimpunctata*.	CAABAAAC	GAD	CAABCA	DE	DBBA	CDB	CBEBA	CDGEDCHJA	DCFDDBACA	EQCDEFA
636.	COL	*Chilocorus bivulnerus**.	CAECABBC	MEA	CAABDA	DB	DBBA	CDB	CFPBA	BCHDBDNQA	DCECJAADA	EOCDEDA
637.	COL	*Coccinella septempunctata*	CACBAAAC	GAD	CAABCA	DB	CBGA	CBE	CBDBA	BCGEDCJKA	DDFDDBACA	EQCDEFA
638.	COL	*Epilachna varivestris*	CABBAAAC	GAD	CAABCA	DE	CBGA	CBI	CBLBA	BDGEDBHJA	DDFDDIACA	EABDEFA
639.	COL	*Microweisea misella**.	CAECABBA	MEA	CAABDA	DE	DBGA	CDI	CFBBA	CCHDBCOGA	BDECBAACA	EQBDEDA
640.	COL	*Endomychus coccineus**	BAECABBC	CEA	BAABDA	DE	CBGA	CDB	CBHBA	BDHDBDNQA	DDFCBHADA	ELBDEDA
641.	COL	*Lycoperdina succinata**.	CAECABAA	OEA	BAABDA	DB	DBGA	CDB	CDKBA	CDHDBDNQA	DCFCBBADA	ELBDEDA
642.	COL	*Mycetaea hirta**	CAECABBA	MEA	BAABDA	DB	DBGA	CDB	CBKBA	BEHDCDNQA	CDFCDCADA	ELBDEDA
643.	COL	*Cartodere costulata**.	CAECABBC	CEA	BAABDA	DE	DBGA	CDI	CBEBA	BDHDBDNQA	DCECJAADA	ELCDEDA
644.	COL	*Hesperobaenus** sp.	CAECAABC	MEA	BAABDA	AA	DBGA	CDI	CBJBA	BDHDCDNQA	DDFBJBADA	ELCDEDA
645.	COL	*Byturus tomentosus**	CAECABBA	MEA	BAABDA	DE	CBGA	CDB	CBHBA	CDHDBDNQA	CDFCBFADA	EFCDEDA
646.	COL	*Mycetophagus punctatus*.	CACBAAAA	GAB	BAABCA	DE	DBGA	CBI	CBEBA	BEGECBHJA	DDFDDBACA	EOBDEFA
647.	COL	*Mycetophagus punctatus**	CAEBABBC	CEA	BAACDA	DE	CBGA	CDJ	CBKBA	BEHDCDNQA	CDFCDHADA	EODDEDA
648.	COL	*Penthe obliquata*.	CACBAAAA	CAB	CAABCA	CB	CBCA	CB	CBDBA	BDGECBJJA	DDFDCFACA	ELBDEFA
649.	COL	*Cis boleti**	BAECABAA	MEA	BAACDA	DB	CBGA	CDI	CBEBA	BDHDJDNQA	CDFCJFADA	ENADEDA
650.	COL	*Melandrya striata**.	CAEBABBA	MEA	BAABDA	DB	DBGA	CDI	CBDBA	BEHDBDNQA	DCEDJAADA	ELCDDFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
651.	COL	_Mordella quadripunctata_	CABBAAAC	FAB	CAABCA	DB	BBGA	CB	CBDBA	BEGEDBGHA	CDEDDAABA	EDBDEFA
652.	COL	_Tomoxia bidentata_	CACBAAAA	CAB	CAABCA	DC	CBJA	CBI	CBDBA	CEGEDBHJA	CDFDCLABA	EDBDEFA
653.	COL	_Macrosiagon ferrungineum_	ECCBAAAA	EAD	CEABCB	CE	CBEA	BBI	CBLBA	CGECBERI	CCFDD A J	KGCBEFC
654.	COL	_Macrosiagon ferrungineum_*	CAECAABC	CEA	CAABDA	AA	DBCA	CDG	COBBA	BBHDCCBBA	CBAAAAAAA	ESBDFDA
655.	COL	_Rhipiphorus dimidiatus_	ECCBAAAA	FAD	CEABCB	DE	CBGA	BBI	CFDBA	CCGECBERI	CDFDDCABJ	KGCBEFB
656.	COL	_Rhizostylops inquirendus_*	CAECAAAC	CEA	CAABDA	AA	DBCA	CDG	COBBA	DCFDCBAAA	CCEBJAADA	ESADFDA
657.	COL	_Pterogenius nietneri_*	CBEBABAA	OEA	BAACDA	DE	CCGA	CRC	CBNBA	BDHDBDNQA	DCFDDBACA	ENCDDDA
658.	COL	_Aulonium tuberculatum_*	CAEBABBA	OEA	BAABDA	DE	CBGA	CDI	CFEBA	DEHDCDNQA	CDFCJBADA	ENCDEDA
659.	COL	_Synchita fuliginosa_*	CAEBABBC	OEA	BAABDA	DE	DBGA	CDI	CBJBA	CEHDCDNQA	CDFCBHADA	EL EEDA
660.	COL	_Hyporhagus texanus_*	CAEBABBA	OEA	BAABDA	DB	DBGA	CBI	CBDBA	BEHDCCNQA	DCFCDBACA	EZBDEDA
661.	COL	_Phellopsis obcordata_*	CAEBABBA	OEA	BAABDA	DB	CBGA	CBI	CBCBA	BEHDBDNQA	CDFCBBADA	EYBDEDA
662.	COL	_Perimylops antarcticus_*	CAEBABBA	CEA	BAABDA	CE	CBGA	CCE	CBLBA	CCHDCDQHA	DCFCDBAEA	EUCDGDA
663.	COL	_Chalcodrya_* sp.	CAEBABAA	OEA	BAACDA	DB	BBBA	CEC	COMBA	CEHDCCNQA	DDFCDHAEA	E&CDEDA
664.	COL	_Alobates pennsylvanica_	CACBAAAA	GAD	BAABCA	DB	DBGA	C I	CBEBA	CDGEDBJKA	DDFDCLACA	EQCDDFA
665.	COL	_Alobates pennsylvanica_*	CAECABBA	OEA	BAABDA	DB	DBMA	CCI	CBEBA	BDHDBDNQA	CDFCBHADA	EVCDDDA
666.	COL	_Arthromacra aenea_	CACBAAAA	GAD	BAABCA	DC	CBCA	C I	CBEBA	BDGEDCHJA	DDFDCLACA	EADODFA
667.	COL	_Holocephala ferruginea_*	CAECABBA	OCA	BAABDA	DB	DBGA	CBI	CBEBA	BDHDBDNQA	DDECBAADA	EBCDDDA
668.	COL	_Hymenorus pilosus_*	CAEBABBA	OCA	BAABDA	DC	DBGA	CBI	CBEBA	BDHDBCNQA	DDFCBFADA	EKCDEDA
669.	COL	_Merinus laevis_*	CAEBAB A	O A	BAABDA	D	DBGA	CBI	CBEBA	BCHDCCNQA	CCFCDHADA	EVCDDDA
670.	COL	_Pimelia cephalotes_	CACBAAAA	FAD	BAABCA	DB	CBGA	CBN	CBEBA	BDGECBHJA	DDFDDBACA	EECDAFA
671.	COL	_Scotobates calcaratus_*	CAEBABBA	OAA	BAABDA	DB	DBGA	CRI	CBEBA	CDHDBCNQA	CDECDAADA	EVCDDDA
672.	COL	_Tenebrio molitor_	CACBAAAA	FAD	BAABCA	DB	DBGA	CHI	CBEBA	BDGECCHJA	DDFDDHACA	EBCDDFA
673.	COL	_Tenebrio_* sp.	CAEBABBA	CCA	BAABDA	DB	DBGA	CBN	CBEBA	BDHDBCNQA	CDFCBFACA	EBCDDDA
674.	COL	_Cephaloon lepturides_	CACBAAAA	CAB	BAABCA	CB	CBCA	CD	CFIBA	BDGECCHJA	CDGDCBJCA	EADFEFA
675.	COL	_Epicauta pennsylvanica_	CACBAAAA	CAD	CAABCA	DE	DBGA	CB	CBIBA	CDGEDBJKA	DDFDCBACA	EACDEFA
676.	COL	_Epicauta pennsylvanica_*	CAECABAA	CCA	BAABDA	DE	DBGA	CB	CFIBA	BDHDJDOGA	DDECJAADA	EQCDEDA
677.	COL	_Leptopalpus rostratus_	CCCBAAAA	CAD	CDABBA	CB	CBNA	BJB	CFEBA	CDGELEKJJ	DCFDDLABK	KGCBEFA
678.	COL	_Macrobasis immaculata_	CACBAAAA	CAB	CAABCA	DB	DBCA	CBE	CBDBA	CDGECBNQA	DDFDCBACA	EACDEFA
679.	COL	_Nemognatha piezata_	CCCBAAAA	CAB	CEABCA	CB	CBNA	BAA	CFEBA	CDGECBEJI	CDFDDIABJ	KGCBEFA
680.	COL	_Zonitis bilineata_*	CAEBABAA	CEA	BAABDA	DE	DBGA	CAI	CFIBA	BBHDCCOGA	DCECJAADA	ESABFDA
681.	COL	_Calopus angustus_*	CAECABBA	OAA	BAABDA	DB	DBGA	CCI	CBCBA	BEHDBCNQA	CDFCBHADA	EZBDEDA
682.	COL	_Nacerdes melanura_*	CAEBABAA	OAA	BAACDA	CC	CBBA	CBC	CBNBA	CCHDBBOGA	CDFCDBACA	RKCDCDA
683.	COL	_Prostomis mandibularis_*	BAEBABAA	OEA	BAABDA	DE	CBGA	CDI	CBEBA	BEHDCCNQA	CDFCDFACA	EUCEEDA
684.	COL	_Synchroa punctata_*	CAECABBA	OEA	BAABDA	DB	DBGA	CDI	CBEBA	BEHDCCNQA	CDFCDHACA	ENCDEDA
685.	COL	_Mycterus curculionides_*	CAEBABAA	CEA	BAABCA	CE	CBBA	CDB	CBEBA	DCHDBCQHA	CCFCDJHDA	EKCDDDA
686.	COL	_Trichentoma childreni_*	CAEBABAA	KAA	BAABDA	DE	BAEA	CBE	CBEBA	BCGDBCHCA	CBFDBBADA	E DDDA
687.	COL	_Pytho americanus_	CABBAAAA	GAD	BAABCA	CE	DBGA	CDC	CFIBA	CDGECBHJA	DDFDDLACA	E FA
688.	COL	_Pytho niger_*	CAECABBA	OEA	BAACDA	DE	DBGA	CC	CBEBA	CEHDBCNQA	CDFCDBADA	EQCDDDA
689.	COL	_Neopyrochroa femoralis_*	CAEBABBC	CEA	BAACDA	DE	DBGA	CCI	CBDBA	CEHDCCNQA	DDFCDBADA	EEDDEFA
690.	COL	_Othnius umbrosus_*	CAEBABBA	OEA	CAABDA	DE	CBGA	CCI	CBEBA	CEHDBDNQA	CDFCBBADA	EVCDDDA
691.	COL	_Aegialites debilis_*	CAECABBA	OEA	BAACDA	DB	DBGA	CBI	CBEBA	CEHDBDNQA	DDFCBHADA	EQCDEDA
692.	COL	_Anthicus_* sp.	CAEBABBA	MCA	BAACDA	AA	DBGA	CBI	CBLBA	CEHDCCNQA	DDFCDHADA	EQCDEDA
693.	COL	_Notoxus calcaratus_	CABBAAAC	CAD	CAABCA	CB	CBGA	CBI	CBDBA	CDGEDBHJA	DDFDCBACA	EQCDEFA
694.	COL	_Scraptia sericea_*	CAEBABAA	OAA	BAABDA	DE	DBGA	CBI	CFDBA	BEHDBCNQA	CDFCBBACA	EVCEDDA
695.	COL	_Cyllene robiniae_	CACCAAAA	CAB	CAABCA	DE	DBNA	C C	CBBBA	BDGEDCHJA	EDDDDLACA	EAADEFA
696.	COL	_Desmocerus palliatus_	CABBAAAA	CAD	CAABCA	DE	DBNA	C C	CDLBA	BEGEDBHJA	DDDDCLACA	EHADEFA
697.	COL	_Leptura_ sp.	CABBAAAA	CAD	CAABCA	DB	DBNA	C C	CBLBA	BDGEDCHJA	EDDDCLABA	EHBDEFA
698.	COL	_Monochamus titillator_	CABBAAAA	CAD	CAABCA	DB	DBNA	C C	CBBBA	BDGECBHJA	EDDDDLABA	RKBDEFA
699.	COL	_Oberea tripunctata_	CACBAAAA	CAB	CAABCA	CB	DBJA	C C	CFBBA	BDGECBHJA	EDFDCHABA	RKEADFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
700.	COL	*Orthosoma** sp.	CAECABBC	BAA	BAABDA	DB	CBGA	CB	CDBBA	BDHDBDNQA	DDFCBBADA	RZCDDDA
701.	COL	*Rhagium** sp.	BAECABBC	MAA	BAABDA	DC	DBGA	CB	CDBBA	BDHDBDDGA	DCFCBBACA	RZCDDDA
702.	COL	*Tetraopes tetraopthalmus*	CABCAAAA	CAB	CAABCA	DB	DBGA	CCE	CFBBA	BDGECBJKA	EDFDDHABA	EEADEFA
703.	COL	*Bruchus discoideus*	CABBAAAC	FAB	EAABCA	DB	DBGA	CBE	CFCBA	BDGECBHJA	DDFDCHACA	ECADEFA
704.	COL	*Bruchus pisorum**	AAEAABBC	MCA	BAABDA	DB	DBGA	CDA	CNBBA	GCHBJDNQA	DCBAAHAAA	RCADEDA
705.	COL	*Atalasis sagroides*	CABBAAAA	CAB	CAABCA	DE	DBGA	C C	CFLBA	CEGECBHJA	DDDDDHACA	EEBDEFA
706.	COL	*Crioceris asparagi**	CAEAABAA	MEA	CAABDA	DB	DBBA	CDE	CRDBA	BBHEJDNQA	DBEBJAADA	EEADEDA
707.	COL	*Galerucella birmanica*	CABBAAAA	FAD	BAABCA	DC	DBBA	CBC	CBHBA	CEGECCJKA	DDFDDBADA	EEADEFA
708.	COL	*Galerucella xanthomelaena**	CAEBABBC	MCA	CAABDA	DB	DBBA	CDE	CRDBA	CCHEJDNQA	DCFCJBADA	EEADEDA
709.	COL	*Hispa testacea**	CAEBABBC	MEA	BAABDA	DB	DBGA	CDE	CRDBA	BBHCJDNQA	DCFCJBADA	EPDDEDA
710.	COL	*Leptinotarsa decemlineata*	CACBAAAC	CAD	CAABCA	DB	DBGA	CBE	CBEBA	BDGEDCHJA	DDFDCHACA	EEBDEFA
711.	COL	*Megamerus kingi*	CABBAAAA	CAB	CAABCA	DE	DBNA	CBC	CBEBA	BEGEDBHLA	EDGDCHACA	EEADEFA
712.	COL	*Phyllotreta nemorum**	CAEBABBA	MAA	CAABDA	DB	DBGA	CDE	CRDBA	BCHDJDNQA	DBBAABAAA	EPDDEDA
713.	COL	*Sphaeroderma testaceum**	CAEBABBC	MCA	CAABDA	DE	DBGA	CDE	CRDBA	ACHCJDNQA	DCBAABAAA	EPDDEDA
714.	COL	*Zeugophora subspinosa**	CAEBABBC	DEA	BAABDA	DB	CBNA	CDE	CRDBA	BCHDBDNQA	DBBAAMAAA	EPDDEDA
715.	COL	*Cimberis attleboides*	DCDDACAC	IAD	CAACFA	DE	CBBA	BBE	FFEBD	BDGECCJKD	DCFDDHACH	RHADEFA
716.	COL	*Araecerus fasciatus*	CBBBAAAC	GAB	CAABCA	DC	DBGA	BAI	CBEBA	CDGEBCNQA	DCDDDHABA	ECCDEFA
717.	COL	*Araecerus fasciatus**	CAECABAA	AAA	CAABDA	DB	CBGA	CBI	CNDBA	CDGCJDJPA	DCEBJAADA	ECBDEDA
718.	COL	*Euparius marmoreus*	CBBBAAAC	GAB	CAABCA	DE	DBGA	BAI	CBEBA	CDGECCJKA	DCDDDHABA	ELADEFA
719.	COL	*Euparius marmoreus**	CAEAABAA	AAA	CAABDA	DB	DBGA	CBI	CNDBA	CDGDJDJPA	DDEBJAADA	ELBDEDA
720.	COL	*Rhopalotria glossoni*	DCDDACAA	HAB	CAACFA	CB	AAAA	BHE	FLDBD	BCHDBDNQD	CCEDDAADH	EBBDEFA
721.	COL	*Dicordylus binotatus*	DCDDAAAA	CAB	BAABCA	AA	AAAA	B B	FLC D	BBGEBDHJD	CCFDBBADH	RADDEFB
722.	COL	*Proterhinus anthracias**	CAEBABCC	MAA	BAABDA	DB	DBGA	CBC	CBDBA	CCHCCDNQA	DCFCDHADA	EEBDEDA
723.	COL	*Rhynchites aenus**	CAEBABBA	MEA	CAABDA	DB	DBGA	CBC	CBDBA	CCHDBDNQA	DDFCBHADA	EFADEDA
724.	COL	*Rhynchites auratus*	DCDDACAA	GAD	CAACFA	DB	AAAA	BBH	FLDBD	BDGDJDHJD	CCFDBHADH	EDADEFA
725.	COL	*Eupsalis minuta*	DCDDACAA	DAD	CAACFA	CB	AAAA	BBE	FRDBD	BCHDBCQHD	CCBAAHAAH	ELDDEFA
726.	COL	*Eupsalis minuta**	CAEBABBA	AAA	CAABDA	DE	DBGA	CBC	CBDBA	CDHCJDNQA	DDFCJBADA	RKADEDA
727.	COL	*Apion strongylodontis*	DCDDACAA	GAB	CAACFA	CB	AAAA	BBE	FLDBD	BCHCBDNQD	CCFBJLADH	EECDEFA
728.	COL	*Ithycerus novaeboracensis*	CBDCAAAA	GAD	BAABCA	DE	AAAA	CBE	CDDBA	CDGDJDIMA	DCFDJHADA	RKCDEFA
729.	COL	*Calandra granaria*	DCDDACAA	IAD	CAACFA	DB	AAAA	BDE	FLDBD	BCGBJDBJD	CCBAAHAAH	ECDDEFA
730.	COL	*Calandra granaria**	CAEBABBA	ACA	CAABDA	DB	DBGA	CBI	CBDBA	CDHCBDNQA	DCFCBHADA	ECCDEDA
731.	COL	*Caulophilus latinasus*	DCDBACAC	IAB	CAABFA	CE	AAAA	BBE	FLDBD	BCHECDNQD	DCFCBHADH	RBAEEFA
732.	COL	*Cionus oleus**	CAECABBA	MEA	CAABDA	DC	DBGA	CBI	CBDBA	CCHBJDNQA	DDEBJAADA	RJBDGDA
733.	COL	*Cionus scrophulariae*	DCDDACAC	IAB	CAACFA	CB	AAAA	BBE	FLDBD	BCHDBDQHD	CCEDBAADH	EEBDEFA
734.	COL	*Curculio caryae*	DDDDACAC	IAD	CAACFA	CE	AAAA	BBE	FLDBD	BCHDJDNQD	BCFCJLADH	RCADEFA
735.	COL	*Dendroctonus valens*	CABCAAAC	IAD	CAACCA	AA	AAAA	BBC	FBDBD	BDHDBCNQD	CCFDBLACH	RKBDEFA
736.	COL	*Eumycteris saccharidis**	CAEAABBA	MCA	CAABDA	DB	DBGA	CBC	CNBBA	CCHCBDNQA	DCFCBBADA	EEADEDA
737.	COL	*Ips concinnus*	CABCAAAC	IAD	CAACCA	AA	AAAA	BBC	FBDBD	BCHDBDNQD	CCEDFAADH	RKADEFA
738.	COL	*Lixus concavus*	DCDDACAC	IAD	CAACFA	CE	AAAA	BBE	FLDBD	BCHDCBNQD	CCFDJBADH	EABDEFA
739.	COL	*Mononychus vulpeculus*	DCDDACAC	IAD	CAACFA	DE	AAAA	BBC	FLDBD	BCHDCCNQD	CCGCJFCDH	RCADEFA
740.	COL	*Pantomorus leucoloma*	CBBCACAA	IAD	CAACFA	DB	AAAA	BBC	FODBD	BCHD CNQD	DCEDBAADH	EECDEFA
741.	COL	*Pissodes strobi*	DCDDACAC	IAD	CAACFA	CE	AAAA	BBE	FLDBD	GDHDBDQHD	CCEDBAADA	RKADEFA
742.	COL	*Platypus australis*	CABBAAAA	IAD	CAACCA	DB	AAAA	BBI	FBLBD	DCGDGDHKD	DCEDBAADH	RLADEFA
743.	COL	*Rhynchaenus alni**	CAEAABBA	MCA	CAABDA	DB	DBGA	CBC	CBDBA	CCHCBDNQA	DCFBJBADA	PEADEDA
744.	COL	*Scolytus piceae*	CABCAAAA	IAB	CAACCA	CE	AAAA	BB	FBDBD	BDHDJDNQD	DCEDBAACH	RKADEFA
745.	STR	*Mengenilla theryi*	BACAAAAA	JAC	CAABBA	DB	AAAA	CAA	CHBBA	BBFCCCAAA	DDFBDCADA	QZEAEFC
746.	STR	*Eoxenos laboulbenei*	BAC AAAA	GAB	CAABBA	DD	CEBA	CAA	CFBBA	AAFCCCAAA	DBAAAAAAA	QZEADFB
747.	STR	*Eoxenos laboulbenei** [male]	BAEAAAAF	MEA	FGABDA	AA	CBBA	DAA	AAAAA	BFCBDAAA	AAAAAAAAA	SSABFDB

	order	taxon	I	II	III	IV	V	VI	VII	VIII	IX	dietary data
748.	STR	Eoxenos laboulbenei* [female]	AAAAAAAF	MEA	FGABDA	AA	DBBA	DAA	AAAAA	AAFBCDAAA	AAAAAAAAA	SSABFDC
749.	STR	Callipharixenos muiri*	CAEAAAAF	MEA	FAABDA	AA	CBBA	CAA	CHBBA	AAFCBDAAA	AAAAAAAAA	SSABFDA
750.	STR	Halictophagus philaroniae	BADAAAAA	JAC	CAABBA	DD	AAAA	CHN	CFBBA	AAFCCDAAA	DBAAAAAAA	QZEAEFC
751.	STR	Halictophagus zanzibarae*	CAEAAAAF	JEA	FAABDA	AA	CBBA	CAA	CDDBA	AAFCBDAAA	AAAAAAAAA	SSABEDB
752.	STR	Elenchus koebeli	BACAAAAA	JAB	CAABBA	CD	DEBA	CHN	CHBBA	BBFCBCAAA	EBAAAAAAA	QZEAEFC
753.	STR	Elenchus koebeli*	CAEAAAAF	MEA	FAABDA	AA	DBBA	CAA	CDBBA	BBFCJDAAA	DBAAAAAAA	SSABEDC
754.	STR	Caenocholax hoberlandti	BACAAAAA	JAC	CAABBA	DD	DEBA	CHN	CHBBA	CBFCCBAAA	EBAAAAAAA	QZEAEFC
755.	STR	Stylops pacifica	BACAAAAA	JAC	CAABBA	DD	DEBA	CBN	CHBBA	CCGCBBBBA	EBAAAAAAA	QZEAEFC
756.	STR	Xenos vesparum	BABAAAAA	JAC	CAABBA	DB	CBBA	CBN	CHBBA	BBFCBCAAA	EBAAAAAAA	QZEAEFC
757.	MEC	Merope tuber	CBDAAAAA	CAB	CAABEA	CD	BEED	CBM	CQIBD	CBGFCBHJD	CDECNAADH	TUCEDFA
758.	MEC	Notiothauma reedi	EBDCAAAA	CDB	CAABEA	CD	BEBD	CBM	CHIBD	DCGFCBHJD	CCECDAACH	T FA
759.	MEC	Chorista australis	CBDAAAAA	CDB	CAABEA	CB	CBBD	CBM	CQDBD	CCGFDCHJD	CCECDAADH	TQCDEFA
760.	MEC	Nannochorista dipteroides	CBBBAAAA	CDB	CFABEA	CD	BEEF	BJD	CAAAD	CCKFCBAIC	CCECKAAEE	JQCDEFA
761.	MEC	Apteropanorpa tasmanica	ECDBAAAA	CAD	CAABEA	CB	DBBD	CBM	CQDBD	DCGFCEHJD	BCECPAADH	TQCDEFA
762.	MEC	Brachypanorpa carolinensis	CBBCAAAA	CDD	CAABEA	CB	CBBD	CBM	CQDBD	CCGFCBGID	DCECDAADH	TECDEFA
763.	MEC	Panorpa communis*	CAEBABBA	DEA	CAABDA	CC	DBCA	CHC	CFLBA	BBGECCHJA	CDEDBAADA	EWCDGDA
764.	MEC	Panorpa nuptialis	ECDCAAAA	CDB	CAABEA	BD	BEGD	CBM	CQDBD	DCGFCBIJD	BCECPAADH	TWCDEFA
765.	MEC	Panorpodes paradoxa	EBDCAAAA	CDB	CAABEA	CD	CECD	CBM	CQIBD	CCGFCBGJD	BCECDAACH	TECDEFA
766.	MEC	Bittacus pilicornis	ECDAAAAA	CDB	CAABEA	CD	BEED	CBM	CHDBD	DCGFCEGJD	BCECDAABH	TQCDEFA
767.	MEC	Bittacus pilicornis*	CAECABAA	DEA	CAABDA	DB	DBCA	CHC	CFEBA	GBHEBCQHA	DDECBAACA	EQCDGDA
768.	MEC	Neobittacus blancheti	ECDAAAAA	CDB	CAABEA	CD	BEED	CBM	CHDBD	DCGFCEGJD	BCECDAABH	TQCDEFA
769.	MEC	Apterobittacus apterus	EBDAAAAA	CDB	CAABEA	CD	BEED	CBM	CHDBD	DCGFBBHJD	CCECBAACH	TQCDEFA
770.	MEC	Apterobittacus apterus*	CAECABAA	DEA	CAABDA	CC	DBCA	CHC	CFDBA	GCHDBDQHA	DCECBAADA	EWCDDDA
771.	MEC	Boreus brumalis*	CAECA BA	MEA	CAABDA	CB	CBMA	CHC	CBDBA	BCHDJDOGA	CBEBJAADA	EEBDDDA
772.	MEC	Boreus nivoriundus	ECDBAAAA	CDB	CAABEA	BD	CEGD	CJM	CQDBD	CBGFCBBBD	CBECJAADH	TEBDDFA
773.	SIP	Anomiopsyllus sp.	CCECAAAA	PAA	CCDBFB	AE	DDHA	AND	AAAAA	EBGECECEG	CCEDQAAFC	BRABFFA
774.	SIP	Hystrichopsyllus gigas	CCECAAAG	PCA	CCDBFB	AE	DDHA	AND	AAAAA	EBGECECEG	CCEEQAAFC	BRABFFA
775.	SIP	Cleopsylla townsendi	CDACAAAG	PAA	CCDBFB	AE	CDHA	AND	AAAAA	EBGECBCEG	CCEEQAAFC	BT BFFC
776.	SIP	Ctenidiosomus traubi	CDACAAAG	PAA	CCDBFB	AE	CDHA	AND	AAAAA	EBGECECEG	CCEEQAAFC	BT BFFA
777.	SIP	Ceratophyllus wickhami*	CAEBAABA	BAA	BAABDA	AE	DBBA	CBC	CFDBA	BBGCCCBMA	CCFBJFADA	EWAEFDA
778.	SIP	Cratynius crypticus	CCECAAAA	PCA	CCDBFB	AE	DDHA	AND	AAAAA	EBGECBCEG	CCEEQAACC	BRABFFA
779.	SIP	Leptopsylla pectiniceps*	CAECAABA	BAA	BAABDA	AE	DBBA	CBC	CFDBA	BCHCCCOGA	CCFBJFADA	BRABFDA
780.	SIP	Nosopsyllus fasciatus*	CAEBAABA	BAA	BAABDA	AE	DBBA	CBC	CFDBA	BCHCCDOGA	CCFBJFADA	EWAEFDA
781.	SIP	Opisodasys pseudarctomys	CCECAAAA	PCA	CCDBFB	AE	DDHA	AND	AAAAA	EBGECECEG	DCEEQAAFC	BRBBFFA
782.	SIP	Sternopsylla distincta	CDECAAAG	PCA	CCDBFB	AE	CDHA	AND	AAAAA	EBGECBCEG	CCEEQAAFC	BRBBFFC
783.	SIP	Malacopsylla grossiventris	CDECAAAA	PCA	CCDBFB	AE	CDHA	AND	AAAAA	EBGECBCEG	BCEEQAABC	BRBBFFC
784.	SIP	Rhopalopsyllus lugubris	CDECAAAA	PCA	CCDBFB	AE	CDHA	AND	AAAAA	EBGECBCEG	CCEEQAABC	BR BFFC
785.	SIP	Ctenocephalides canis	CCECAAAG	PCA	CCDBFB	AE	CDHA	AND	AAAAA	EBGECCCEG	BCEEQAACC	BRABFFA
786.	SIP	Ctenocephalides felis	CCECAAAG	PCA	CCDBFB	AE	CDHA	AND	AAAAA	EBGECBCEG	CCEEQAACC	BRABFFA
787.	SIP	Ctenocephalides felis*	CAEBAABA	BAA	BAABDA	AE	CBBA	CBC	CFDBA	BCFBIDAAA	AAAAAAAAA	EWAEFDA
788.	SIP	Echidnophaga gallinacea	CCECAAAA	PCA	CCDBFB	AE	DDHA	AND	AAAAA	EBGECBCEG	DCEBQAACC	BRCBFFA
789.	SIP	Pulex irritans	CCECAAAA	PCA	CCDBFB	AE	DDHA	AND	AAAAA	EBGECECEG	CCEDQAABC	BRCBFFA
790.	SIP	Xenopsylla cheopis	CCECAAAA	PCA	CCDBFB	AE	DDHA	AND	AAAAA	EBGECBCEG	CCEEQAABC	BRABFFA
791.	SIP	Xenopsylla cheopis*	CAEBABBA	BAA	BAABDA	AE	DBCA	CBC	CFDBA	BCGCCDBMA	BCFBJCADA	EWAEFDA
792.	SIP	Tunga penetrans	CDECAAAA	PCA	CCDBFB	AE	CDHA	AND	AAAAA	EBGECBCEG	CCEEQAABC	BTCBFFC

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
793.	DIP	*Trichocera bimaculata*	CBCAAAAA	BDB	CFABFB	DB	CBEF	BHC	AAAAA	DCKFCEAJC	DCECKAAEE	J FC
794.	DIP	*Trichocera** sp.	CAECABBH	MAA	BAABCA	CB	DBBA	CBC	CBLBA	GCHCJDDGA	DBBAAAAAA	EVCDDDA
795.	DIP	*Dicranomyia* sp.	ECDDAAAA	CAB	CFABFB	BE	BDEF	BGE	AAAAA	CBKECEAPC	BCDCKIAEE	JGCAEFA
796.	DIP	*Dicranota** sp.	DAEBABBC	OAA	BAABCA	DB	DBBA	CBC	CFJBA	CCHBJDDGA	DBBAABAAA	EQCDBDA
797.	DIP	*Eriocera** sp.	DAEBABBC	OAA	BAABCA	BB	DBBA	CBC	CFBBA	CCFBBCAAA	AAAAAAAAA	EQCDBDA
798.	DIP	*Erioptera* sp.	CBBDAAAA	CAB	CFABFB	CE	BDEF	BGE	AAAAA	CBFECEAAC	DCDCKFAEE	JGCAEDA
799.	DIP	*Geranomyia rufescens*.	EDDDAAAA	CAB	CFABFB	BE	BDCF	BGE	AAAAA	DBKBBDAPC	BCDBBFAFA	BACBEFC
800.	DIP	*Holorusia rubignosa**.	CAEBABBC	OCA	BAABCA	BB	CBJA	CBC	CFBBA	BCFBJDAAA	DBBAAAAAA	E*CCBDA
801.	DIP	*Limnophila* sp.	CBBDAAAA	CAB	CFABFB	CE	EF	BGE	AAAAA	CBKECEAPC	DCDCKFAEE	JGCAEFA
802.	DIP	*Tipula livida**.	CAEBABBC	OAA	BAABCA	BB	DBCA	CBC	CFDBA	GEHBJDQHA	DBBAAAAAA	E&CEBDA
803.	DIP	*Tipula reesi*.	ECDDAAAA	CAB	CFABFB	BE	BDCF	BEE	AAAAA	DBFECEAAC	BCDCKAAEE	JGCAEFA
804.	DIP	*Protoplasa fitchii*.	ECCBAAAA	CAB	BFABFB	CB	BBCF	BEC	CMBAA	DBKFCEACC	CCECKAAEE	J%EAEFA
805.	DIP	*Protoplasa fitchii**	CAEBABBC	OCA	BAABCA	DE	DBGA	CBC	CBLBA	BCHBJDNQA	DBBAAAAAA	EUCEBDA
806.	DIP	*Tanyderus forcipatus*.	CCBAAAAA	CAB	BFABFB	CB	BBDF	BEC	CMBAA	BBKFCEACC	BCECKAAEE	J%EAEFA
807.	DIP	*Bittacomorpha clavipes*. . . .	CCBBAAAA	BAB	CFABFB	CB	CB F	BHC	AAAAA	CBFFCEAAC	CBECKAAEE	JACBEFC
808.	DIP	*Bittacomorpha clavipes** . . .	CAEBABBC	MCA	BAABFA	CE	DBGA	CRN	CDLBA	GEHBJDQHA	CBEBJAADA	E&CDBDA
809.	DIP	*Liriope lenis*	CCBBAAAA	BAB	CFABFB	CB	CBEF	BHC	AAAAA	CBKFBEAPC	DBECKAAEE	JACBEFC
810.	DIP	*Ptychoptera rufocincta*. . . .	CBCBAAAA	CAB	CFABFB	CB	CBBF	BHC	CMBAA	CBFFBEAAC	DBECKAAEE	JACBEFC
811.	DIP	*Ptychoptera lenis**.	CAECABBC	MAA	BAABCA	DE	DBNA	CHK	CDLBA	BCGBJDIJA	DDBAALAAA	E&CDBDA
812.	DIP	*Lutzomyia flaviscutella* . . .	ECD AAAA	CAB	CCFBFA	CB	EBFE	AGD	BIIDC	CBKFCEAEH	BCECKAAED	ARCBFFB
813.	DIP	*Phlebotomus papatasii*	ECBBAAAA	CAB	CCFBFA	CB	EBIE	AGD	BIIDC	DCKFCEAEH	BCDCKBAED	ARCBFFB
814.	DIP	*Psychoda albipennis*	CBBAAAAA	DAB	CCEBFA	CE	BBIE	AGD	AAAAA	DBKECBAEH	BCECKAAED	AUCBEFA
815.	DIP	*Psychoda sexmaculata**	CAEBABBA	NCA	BAABCA	CB	CBNA	CF	AAAAA	CBDAAAQHA	EBBAAAAAA	M*CCBDA
816.	DIP	*Dixa clavata*.	CBBAAAAA	BAB	CCFBFA	CE	BBDE	AGD	BIBDC	DCKFCEAEH	BBDCKMAED	AGCBEFA
817.	DIP	*Dixa maculata**.	CAEBABBA	OCA	BAABCA	AA	CBGA	CRK	CCLBA	CBHCCCQHA	CBBAAAAAA	E*CCBDA
818.	DIP	*Australomochlonyx nitidus**. .	CAEBABBH	ECD	BAABCA	DE	CBNA	CRK	CBFBA	BBFDGDAAA	DCBAAHAAA	L*CCBDA
819.	DIP	*Corethella appendiculata*. . .	CCCBAAAA	NAB	CCFBFA	BB	EBDE	AGD	BIIDC	DBKFCBAEH	BBDCKLAED	ARCBFFB
820.	DIP	*Eucorethra underwoodi**. . . .	CAEBABBH	NCD	BAABCA	AE	DBBA	C N	CCFBA	GBHBJDQHA	DCBAAHAAA	EQCDBDA
821.	DIP	*Aedes aegypti*	EDCBAAAA	EAB	CCFBFA	CE	EBDE	AGD	BIBDC	DBKECBAEH	BBDCKMAED	ARABFFB
822.	DIP	*Aedes communis**	CAEBABBH	NCD	BAABCA	AE	DBNA	CRK	CCFBA	BBHBJDNQA	DBBAALAAA	M*CCBDA
823.	DIP	*Anopheles maculipennis*. . . .	EDBBAAAA	CAB	CCFBFA	CE	EBDE	AGD	BIIDC	DBKECEAEH	BBDCKBAED	ARCBFFB
824.	DIP	*Anopheles quadrimaculatus**. .	CAEBABBH	NCD	BAABCA	AE	CBNA	CBK	CCLBA	BCHBBDPQA	DBBAANAAA	M*CCBDA
825.	DIP	*Armigeris malayi**	CAEBABBH	NCD	BAABCA	AE	DBNA	CBG	CBDBA	BBHDBCLLA	DCBAALAAA	M*CCBDA
826.	DIP	*Culex pipiens*	EDCBAAAA	EAB	CCFBFA	CE	EBDE	AGD	BIBDC	DBKDDCAEH	BBDCKMAED	ARCBFFB
827.	DIP	*Culex pipiens**.	CAEBABBH	NCD	BAABCA	AE	DBNA	CRK	CBDBA	BBHBCDQHA	DCBAALAAA	M*CCBDA
828.	DIP	*Culiseta annulata*	EDCBAAAA	EAB	CCFBFA	CE	EBDE	ASD	BIBDC	DCKDCBAEH	BBDCKMAED	ARCBFFB
829.	DIP	*Culiseta incidens**.	CAEBABBH	NCD	BAABCA	AE	DBNA	CRK	CCFBA	BBKBJDDGA	BCBAALAAA	M*CCBDA
830.	DIP	*Lutzia halifaxi**.	CAEBABBH	NCD	BAABCA	AE	DBNA	CRK	CBDBA	BBHCBDLLA	DCBAALAAA	EQCDDDA
831.	DIP	*Psorophora ciliata*.	EDBDAAAA	BAB	CCFBFA	CE	EBDE	AGD	BIIDC	DBKCCBAEH	BBDCKMAED	ARCBFFB
832.	DIP	*Thaumalea testacea**	CAEBAABA	MCA	BAABBA	BE	BBNA	CHE	BBLBA	CBDAAANQA	DBBAAAAAA	M*CCBDA
833.	DIP	*Cnephia dacotensis*.	CBBBAAAA	DAB	CFABFA	CB	BBIE	ABM	CHBBC	CBKFCBARC	DCDCKBAED	TCGBFFB
834.	DIP	*Crozetia crozetensis**	DAEBABAA	NAD	BAABCA	CE	BENA	CHC	CCFBA	ABGBBDIKA	DCBAAHAAA	L*CCBDA
835.	DIP	*Eusimilium lascvium*	CBCBAAAA	DAB	CFBBFA	CB	CBEE	AGE	CHBBC	CBKECCARC	DCDCKMAED	TGCBFFB
836.	DIP	*Parasimilium stonei**.	CAEBABAA	BCA	BAABBA	AE	DENA	CBK	BQFBA	BBHBJDQHA	DBBAAAAAA	L*CCBDA
837.	DIP	*Simulium damnosum*	CBCCAAAA	DAB	CFFBFA	CE	BBIE	AGD	CHIDC	BCKFCEAEC	DCDCKCAED	URCBFFB
838.	DIP	*Simulium venustum**.	CAEBABAA	BEA	BAABBA	CE	DENA	CHC	BQLBA	BBGBBCHRA	DCBAAHAAA	L*CCBDA
839.	DIP	*Atrichopogon pavidus*.	CBBCAAAA	DCB	CCFBFA	CB	EBGE	AGD	CHIDC	ECKFCBAEH	DBECKAAED	UQCBEFB
840.	DIP	*Culicoides nubeculosus** . . .	CAEBABBA	MCA	BAABCA	BE	CBBA	CQE	CDBEA	BBGCJDBCA	CBAAAAAAA	P*CDDDA
841.	DIP	*Culicoides pulicaris*.	CCBBAAAA	CCB	CCFBFA	CE	EBIE	AGD	CHIDC	CCKFCEAEH	BCDCKMAED	URCBFFB

	order	taxon	mouthpart morphology data I	II	III	IV	V	VI	VII	VIII	IX	dietary data
842.	DIP	*Dicrobezzia venusta*	CBBBAAAA	CCB	CCFBFA	CE	BBIE	AGD	CHIDC	EBKFCBAEH	DBDCKBAED	UQCBEFB
843.	DIP	*Schizohelea leucopezia*	CBB AAAA	DCB	CCFBFA	CB	EBIE	AGD	CHIDC	EBKFCBAEH	DBDCKBAED	UQCBEFB
844.	DIP	*Wilhelmia equina*	CBBBAAAA	DAB	CCFBFA	CB	CBIE	AGD	CHIDC	CBKFBEAEH	DBDCKBAED	UQCBEFB
845.	DIP	*Chironomus plumosus**	CAEBABBA	BEA	BAABBA	CE	CBGA	CFC	BFLBA	BBHCJDNGA	DCBAAHAAA	MVCDBDA
846.	DIP	*Glyptotendipes glaucus**	CAEBABBA	NEA	BAABBA	CE	CBGA	CFG	BFLBA	GBHBJDQHA	DBBAAAAAA	L*CCBDA
847.	DIP	*Macropelopia nebulosa**	CAEBABBA	NEA	BCABBA	CE	DBBA	CFE	CFDBA	BBHBJDQHA	EBBAAAAAA	EQCDBDA
848.	DIP	*Prodiamesa olivacea**	CAEBABBA	NEA	BCABBA	CE	DBGA	CFC	CFLBA	CBHBJDQHA	DBBAAAAAA	M*CCBDA
849.	DIP	*Perissosomma fusca**	CAECABBA	MAA	BAABCA	CB	BBNA	CRG	CBLCA	BBDAAAOGA	BBFCJBIDA	GOAEEDA
850.	DIP	*Pergratospes holoptica**	CAEBABBA	MCA	BAABBA	CE	DBGA	CMC	CBDBA	BCHBJDNQA	DBBAAAAAA	EZCDEDA
851.	DIP	*Axymyia kerteszi**	CAEBABBA	ACA	BAABBA	DB	CBGA	CQB	CBJBA	BBHCJDNQA	DBBAAAAAA	EZCDEDA
852.	DIP	*Anisopus fenestralis*	CBBBAAAA	CDB	CFEBFB	BE	CBDF	AGD	AAAAA	DBKFHBAEC	CCDCKBAED	BGCBEFC
853.	DIP	*Mycetobia punctata*	CBCCAAAA	FDB	CFEBFB	CE	CBDF	AGD	AAAAA	EBKDHCAEC	DBDCKBAED	BICBEFA
854.	DIP	*Olbiogaster** sp.	CAECABBA	MAA	BAACBA	BE	CBIA	CHG	CODEA	BCGBJDBJA	CDDBJFADA	PUCDDDA
855.	DIP	*Rhyphus punctatus*	CBCBAAAA	DDB	CFEBFB	DE	CBIF	BGD	AAAAA	CCKFHBAEC	CCDCKBAED	BGCBEFA
856.	DIP	*Bibio femoratus*	CBCBAAAA	DDD	CFABFB	DE	CBCF	BEC	AAAAA	CBFFEBAAC	CBDCKBAED	JDCBEFB
857.	DIP	*Bibio** sp.	CAECABBA	ACA	BAABBA	DE	DBFA	CCG	CBLBA	BDHCJDNQA	CDBAACAAA	EVCDDDA
858.	DIP	*Synneuron decipiens**	CAECADBA	MAA	BAABCA	AA	AAAA	CAA	AAAAA	AAFBJDAAA	AAECAAADA	SZCDEDA
859.	DIP	*Clinodiplosis cilicrus**	AAFEADBA	OBA	BAABFA	CB	CBEA	CQC	COIEA	BBDAAAOGA	DBBAAAAAA	DVABEDA
860.	DIP	*Dasyneura mikii**	AAFEADBA	OAA	BAABFA	CB	CBBA	CQ	COIEA	BBHBADOGA	DBBAAAAAA	DVABEDA
861.	DIP	*Lestodiplosis mikii**	AAFEADBA	OBA	BAABFA	CB	CBFA	CQC	COIEA	CBDAAAOGA	CCBAAAAAA	DQBBEDA
862.	DIP	*Phaenobremia aphidimyza**	AAFEADBA	OAA	BACBFA	CB	CBEA	AQE	COIEA	BBHBADOGA	DBBAAAAAA	DQBBEDA
863.	DIP	*Rhabdophaga strobiloides*	CBBBAAAA	DDB	CFABBB	CE	BBEF	BQE	AAAAA	ECFECBAAC	DBDCKBAEE	JYBBEFB
864.	DIP	*Sciara varians*	CBCAAAAA	CDB	CFABFB	CE	CBDF	BQE	AAAAA	DBKDCCAPC	DCECKAAEE	JUCBDFB
865.	DIP	*Sciara** sp.	CAEBABBA	BCA	BAABBA	CB	DBCA	CCG	CCDBA	CBDAAALLA	DBBAAAAAA	ENCDEDA
866.	DIP	*Epidapus scabiei**	CAEBABBA	MDA	BAABBA	CE	CBCA	CBC	CCDBA	BCHBJDLLA	DBBAAAAAA	EVADGDA
867.	DIP	*Mycetophila divergens*	CBCAAAAA	FCB	CFABFB	CB	CBEF	BBC	AAAAA	DBKECBABC	CCECKAAEE	JGCBEFB
868.	DIP	*Agathon* sp.	CCBCAAAA	CDE	CCFBFA	BE	BBEE	AGD	BIIDC	CCKFCBAEH	DCDCKMAED	QZEAEFA
869.	DIP	*Bibiocephala elegantula*	EBBCAAAA	CDE	CCFBFA	BE	BBDE	AGD	BIIDC	CCKFCBAEH	CCECKAAED	ARCBEFB
870.	DIP	*Edwardsina* sp.	CCCBAAAA	CDE	CCFBFA	CE	BBEE	AGD	BIIDC	CCKFCBAEH	CCDCKMAED	ARCBEFB
871.	DIP	*Liponeura cinerascens*	CBBCAAAA	CDE	CCFBFA	CB	EBDE	AGD	CIIDC	CBKDCEAEH	BCECKAAED	UQCBEFB
872.	DIP	*Deuterophlebia inyoensis**	DAEBABBA	CA	BAABBA	CE	CBGA	C N	BQFBA	BBHBJDPQA	AAAAAAAAA	M*BCBDA
873.	DIP	*Nymphomyia alba*	CBEBAAAA	GCD	BCABDA	AE	AAAA	BAA	AAAAA	AAAAAAAAA	ABEAJAADD	QZEAEFC
874.	DIP	*Glutops rossi**	AAFEADBH	NAA	CAABDA	BE	BBGA	C E	CJBBB	BBKBJDANB	BCBAAAAAA	DQCDGDA
875.	DIP	*Chrysopilus auratus*	CBBCAAAA	KDB	CFCBBB	CB	BBBF	AQE	AAAAA	DBKBGCAEC	CBDCKMAEE	BQBBEFC
876.	DIP	*Chrysopilus** sp.	AAFEADBA	OAA	CAABFA	CE	BBEG	CQC	CEBEB	CBHCJDPNB	BCBAAAAAA	DUCBDDA
877.	DIP	*Rhagio scolopaceus**	AAFEADBA	OAA	CAABFA	CE	BBIG	CRG	CEBEB	BBGCBCPNB	BCEBBAADA	D=CEDDA
878.	DIP	*Rhagio vertebratus*	CBBBAAAA	KDB	CFEBBB	CE	BBEE	AGD	AAAAA	DBKBGCAEC	DBECKAAEE	AQCBEFB
879.	DIP	*Symphoromyia atripes*	CBBBAAAA	KDB	CFFBBB	BE	EBEE	AGD	CIBDC	CCKCGCAEC	DBDCKMAEE	BRCBFFB
880.	DIP	*Vermileo vermileo*	CBCCAAAA	KDB	CFCBBB	BE	BBBF	AQE	AAAAA	CBKCCBAEC	DBDCKMAEE	BQCBFFB
881.	DIP	*Xylophagus abdominalis**	AAFEADAA	ACA	CAABFA	BE	CBGA	CHK	CEBEB	CBKCCCANB	BCBAAAAAA	DQCDEDA
882.	DIP	*Chloromyia formosa**	AAFEBDBH	MAA	BAABFA	BE	CBNA	CJK	CEFBB	EBGCJDIKB	DBBAAHAAA	L*BCBDA
883.	DIP	*Hermetia illucens**	AAFEBDAH	MCA	BCABFA	BE	BBFA	CJC	AAAAA	BBHBJDNQA	BCBAAAAAA	LUCEDFB
884.	DIP	*Odontomyia limbata**	AAFEBDAH	NCA	CAABFA	BE	CBGA	CJC	CEFBB	EBGBCCIKB	CCBAAAAAA	LVCEBDA
885.	DIP	*Oxycera pygmaea**	AAFBEBDH	NCA	CAABFA	BE	BBGA	CJC	CEFBB	EBGBCDIKB	CCBAAAAAA	L*BCBDA
886.	DIP	*Sargus bipunctatus**	AAFEBDAH	MCA	CAABFA	BE	CBGA	CJC	CEFBB	EBGBCDIKB	CCBAAAAAA	LUCEDDA
887.	DIP	*Stratiomys apiculata*	CBBCAAAA	IDB	CFCBBA	CE	ECCF	AQC	AAAAA	BBKCCCADC	DCECKAAEE	JGCBEFB
888.	DIP	*Stratiomys chamaeleon**	AAFEBDBH	MCA	BCABFA	BE	BENA	CRC	CEFBB	EBGBBCIKB	CCBAAAAAA	LUCDBDA
889.	DIP	*Chrysops vittatus*	CCBBAAAA	CDB	CCEBBA	CE	EBFE	AQL	CHIDC	CBGCCCBEH	CBECKAAED	URCBFFB
890.	DIP	*Corizoneura longirostris*	EDCBAAAA	KDB	BCEBBA	BE	EBEE	AGD	CIIDC	DBGCCCEEH	CBECKAAED	ARCBEFB

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
891.	DIP	*Haematopota pluvialis*	CBBBAAAA	KAB	CFFBFA	CE	EBIE	AGD	CHIDC	DCGCCCBEC	CBECKAAEE	URCBEFB
892.	DIP	*Tabanus atratus**	AAFEADBH	NAA	CAABDA	BE	BBDA	C C	CJBBB	CBKBCDANB	BCBAAAAAA	DQCDGDA
893.	DIP	*Tabanus giganteus*	CCBBAAAA	KAB	CFFBBA	CE	EBIE	AGD	CHIDC	CCGCCCBEC	CCECKAAED	URCBFFB
894.	DIP	*Pantophthalmus comptus*. . . .	CBCCAAAA	BDB	CFABBA	CE	AAAA	BQE	AAAAA	BBJCCBAAC	CCECKAAEE	QZEAEFB
895.	DIP	*Neorhynchocephalus sulphureus**	AAFEADBA	AAA	BAABFA	BE	BEEA	CMC	COMEA	BBFBJDAAA	CBBAAAAAA	DSABFDA
896.	DIP	*Lasia* sp.	EDCCAAAA	CDB	CCCBBA	CE	EBDF	AHE	AAAAA	DBKBJDAIH	BCECLAACD	IGCBEFB
897.	DIP	*Ogcodes costatus*.	CACCAAAA	KDB	CCABBA	CE	AAAA	DBA	AAAAA	AAAAAAAAA	AAAAAAAAA	QZEAEFB
898.	DIP	*Dioctria albius*	CCCCAAAB	CDB	BCBBFA	CE	BBEE	AGE	AAAAA	DBKCGCAIH	DCDCQMACD	AQCBEFB
899.	DIP	*Laphria** sp.	AAFEADBA	MAA	CAABFA	DE	BBDA	CBC	CFBEB	BCGCCCBBB	EBBAAAAAA	DQCCEDA
900.	DIP	*Machimus atricapillus*	CCBCAAAB	KDB	BCBBFA	CE	CBEF	AGE	AAAAA	DBKBGCAIH	DCDCQMACD	AQCBEFC
901.	DIP	*Proctacanthus* sp.	CCBCAAAB	KDB	BCBBFA	E	BBDF	AGE	AAAAA	CBKBGCAIC	CCDCQBACE	AQCBEFB
902.	DIP	*Promachus vertebratus*	CCBCAAAB	KDB	BCBBFA	CE	BBDF	AGE	AAAAA	DBKBGCAIH	CCDCQMACD	AQBBEFB
903.	DIP	*Promachus vertebratus**. . . .	AAFEADAA	MAA	BAABFA	CE	BBDA	CME	CFBEB	BBKBJDANB	CBBAAAAAA	EQBDGDA
904.	DIP	*Mydas clavatus*.	CBCBAAAA	GBB	CFEBBA	CE	BCCF	AGD	AAAAA	DBKBJDAEC	DCECKAAEE	UQCDEFB
905.	DIP	*Mydas clavatus**	AAFEADBA	AAA	BAABFA	BE	BBBA	C C	CJBEB	BBKBJDALB	CCBAAAAAA	DQCDDDA
906.	DIP	*Psilocephala haemorrhoidalis*.	CBBBAAAA	KDB	CFEBBB	BE	BBEF	AGD	AAAAA	BBKBCCAEC	CCECKAAEE	JGCBEFC
907.	DIP	*Thereva furcata**.	AAFEADBA	MAA	BAABFA	BE	BBEA	CME	CFBEB	BBGBJDJNB	CCFBJBADA	EQBDGDA
908.	DIP	*Scenopinus fenestralis*. . . .	CBCBAAAA	CDB	CFCBBB	CE	CBBF	ABE	AAAAA	CBKBCCADC	DBECKAAEE	J EFB
909.	DIP	*Exoprosopa fasciata*	EDBBAAAA	KDB	BCCBBA	CE	EBDF	AGE	AAAAA	CBKBGEAEH	BCDCQMACK	BGCBEFB
910.	DIP	*Toxophora virgata*	EDCBAAAA	KDB	BCCBBA	CE	EBDF	AGE	AAAAA	DBKBGBAEH	BCDCQMACK	BGCBEFB
911.	DIP	*Apiocera maritima**.	AAFEADBA	MAA	CCABFA	AA	EBDA	CQC	CFBEB	BBKCJDARB	DCBAAAAAA	UQCDGDA
912.	DIP	*Empis livida*.	ECBBAAAA	KDB	CCCBBA	CE	EB F	AGE	AAAAA	DBKBCBAEC	BCDCQMACD	AQCBEFB
913.	DIP	*Hemerodromia** sp.	AAFEADBA	MAA	BAABFA	BE	EBDA	CRE	CFBEA	AAGCCCJNA	BBBAAAAAA	DQCDBDA
914.	DIP	*Dolichopus bifractus*.	CBCBAAAA	LDB	CFBBBA	CE	CBIF	AED	AAAAA	DBFBDDAAC	CBECKAAEE	BQCBEFB
915.	DIP	*Dolichopus ramifer**	AAFEADBA	MAA	BAABFA	CD	BBEA	CME	CFBEB	BBKCJDANB	CBBAAAAAA	DQBBEDA
916.	DIP	*Medeterea** sp.	AAFEADBA	MAA	BAABFA	DD	BBEA	CME	CFBDB	CBKBJDANB	CBBAAAAAA	DQBDEDA
917.	DIP	*Melanderia mandibulata*. . . .	CACBAAAA	LDD	CAABCA	CB	DBBA	CEG	AAAAA	BBFBGDAAH	DCEC AADA	EQCBEFC
918.	DIP	*Systenus albimanus**	AAFEADBA	MCA	BAABFA	DD	BBEA	CCM	CFBEB	AAKBJDANB	CBBAAAAAA	DQADCDA
919.	DIP	*Lonchoptera lutea*	CCBAAAAA	LDD	CFABBB	AE	CBEF	BBE	AAAAA	AAKBDBADC	CBDCKMAEE	JGCBEFB
920.	DIP	*Platypeza velutina*.	CBCCAAAA	LDB	CFABBB	CE	CBBF	BBE	AAAAA	DBFBDDAAC	CBECKAAEE	JUCBEFB
921.	DIP	*Ironomyia nigromaculata* . . .	CCB AAAA	LDB	CFEBBB	DE	BCEF	AGD	AAAAA	CBKBDDAEC	CCECKAAEE	A EFB
922.	DIP	*Sciadocera rufomaculata**. . .	AAFEAABA	MAD	BAABFA	AA	CBEA	CMG	COBEA	AAHBJDLLA	DBBAAAAAA	DWCDDDA
923.	DIP	*Megaselia agarici*	CBCBAAAA	LDD	CCHBBB	DE	CBDF	BBE	AAAAA	CBFBFCAAC	CCDCLMAEO	JUCBEFB
924.	DIP	*Phora curvinervis*	CBC AAAA	LDB	CCHBBB	CE	CBIF	BEE	AAAAA	BBFBDCAAC	CCECLAAEO	JUCBEFC
925.	DIP	*Eristalis arbustorum*.	CCBBAAAA	LDB	CFBBBB	DE	ECIF	AGK	AAAAA	CBKBBBAIC	BCECKAACE	KGBBEFC
926.	DIP	*Eristalis tenax**.	AAFEAABA	MAA	BAABFA	AD	AEFA	CAE	C FBA	AAFBJDAAA	DDBAAAAAA	L*CCBDA
927.	DIP	*Eumerus strigatus**.	AAFEADBA	MAA	BAABFA	AE	AE A	CRA	C FBA	AAFBJDAAA	DDBAAAAAA	LVACGDA
928.	DIP	*Myathropea florea**.	AAFEADBA	MAA	BAABFA	CE	AE A	CAA	C FBA	AAFBJDAAA	DDBAAAAAA	LVACBDA
929.	DIP	*Rhingia nasica*.	ECCBAAAA	LDD	CFABFB	E	ECIK	BHF	AAAAA	DBKCBEAIC	BCECQAACE	KHBCEFB
930.	DIP	*Pipunculus cingulatus*	CBCBAAAA	LDB	CFABBB	BE	CBBF	BBE	AAAAA	DBFBDBAAC	CBECKAAEE	JGCBEFB
931.	DIP	*Conops brachyrhynchus*	EDBBAAAA	KAB	CFABFB	BE	ECDF	BQE	AAAAA	DBBAAAABC	BCECKAAEE	JGCBEFA
932.	DIP	*Euaresta aequalis*	CCBBAAAA	LDB	CFABFB	BE	BCBF	BBE	AAAAA	DBKBCCAAC	CCECKAAEE	JVCBEFA
933.	DIP	*Toxotrypana curvicauda** . . .	AAGEADBA	MAA	CHCBBB	CE	CBBA	AMA	CJBDB	AAFBJDAAB	DBBAAAAAA	DFBEEDA
934.	DIP	*Physiphora demandata*.	CCBCAAAA	LDB	CFABFB	CE	BCBF	AQE	AAAAA	DDKBCCAAC	CCECKAAEE	JUCBEFA
935.	DIP	*Tritoxa incurva**.	AAFEADBA	MAA	CHCBBB	BE	BBEA	AMA	CJBDB	AAFBJDAAB	DBBAAAAAA	DJAEEDA
936.	DIP	*Eumetopia rufipes**.	AAFEADBA	MAA	CHCBBB	BE	BBBA	AMA	CJBDB	AAAAAAAAA	DBBAAAAAA	DCAEEDA
937.	DIP	*Platysoma seminationis*. . . .	CCBCAAAA	LDB	CFABFB		CCEF	BQE	AAAAA	DBKBDDAAC	CCECKAAEE	JUCBEFA
938.	DIP	*Ozaenina diversa*.	DCCBAAAA	LDB	CFABFB	BE	F	BQE	AAAAA	D KBCCAAC	CCECKAAEE	JUCBEFA
939.	DIP	*Palloptera saltum*	CCBCAAAA	LDB	CFABFB		BCDF	BQE	AAAAA	DBKBCCAIC	CCECKAAEE	JUCBEFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
940.	DIP	*Piophila casei**	AAFEADBA	MAA	CHCBBB	AA	BBBA	AMA	CJBDB	AAFBJDAAB	CDBAALAAA	DWCEFDA
941.	DIP	*Neottiophilum praeustum**	AAFEADBG	MAA	CHCBBB	BE	CBBA	AMA	CJBDB	AAFBJDAAB	DCBAAAAAA	DWCEFDA
942.	DIP	*Lonchaea chorea**	AAFEADBA	AAA	BAABFA	BE	AE A	CMA	COBEA	AAFCJDAAA	CBBAAAAAA	BUCEDDA
943.	DIP	*Cypselosoma australis**	AAFEADBA	MAA	BHCBBB	BE	BBFA	AMA	CJBDB	AAFBJDAAB	DBBAAAAAA	DXABDDA
944.	DIP	*Pseudopomyza atrimana*	CCBCAAAA	LDB	CFABFB	BE	BCBF	BQE	AAAAA	DBFBDCAAC	CCECKAAEE	J BEFA
945.	DIP	*Glyphidops filosus*	CCB AAAA	KDB	CCABFA	BE	ECEF	BQE	AAAAA	DBKBCCAIC	CCECKAAEE	CFBBEFA
946.	DIP	*Compsobata univitta*	CCCCAAAA	LDD	CFABFB	CE	BCMF	BQE	AAAAA	DBKBDCARC	CCECKAAEE	CQCBEFA
947.	DIP	*Nothybus longithorax*	CCBCAAAA	LDB	CFABFB	CE	BCDF	BQC	AAAAA	DCFBCBAAC	CECKAEE	JG BEFC
948.	DIP	*Sphyracephala brevicornis*	BCBCAAAA	LDC	CFABFB	AE	CCEF	BQE	AAAAA	CDKBCCARH	CCECKAAEE	JEBBEFA
949.	DIP	*Teleopsis bigoti*	BCBBAAAA	LDC	CFABFB	CE	BBEF	BM	AAAAA	CCKBCCARC	CCECKAAEE	JGCBEFC
950.	DIP	*Tanypeza longimana**	AAFEADBA	MAA	BAABFA	AA	AAAA	CMA	COBEA	AAFBJDAAA	DBBAAAAAA	DVCDEDA
951.	DIP	*Loxocera pectoralis*	CCCBAAAA	LDB	CFABFB	CE	BCEF	BQC	AAAAA	DBKBCCABC	CCECKAAEE	JQ BEFB
952.	DIP	*Dryomyza analis**	AAFEADBA	AAA	BHCBBB		AAA	AMA	CJBEB	AAFBJDAAB	DBBAAAAAA	DXCEDDA
953.	DIP	*Coleopa vanduzeii*	CCBCAAAA	LDB	CFABFB	CE	CCEF	BQE	AAAAA	DDKBGCABC	CCECKAAEE	JEBBEFA
954.	DIP	*Tetanocera plumosa*	CCBCAAAA	LDB	CFABFB	CE	BCEF	BQE	AAAAA	DDKBCBABC	CCECKAAEE	JUCBEFA
955.	DIP	*Leucopis verticalis**	AAFEADBA	OAA	BAABFA	AA	AAAA	CMA	COBEA	AAFBJDAAA	AAAAAAAAA	DQADEDA
956.	DIP	*Ochthiphila juncorum*	CCCBAAAA	LDD	CFABFB	E	BCCF	BQE	AAAAA	DBKBCCABC	DCECKAAEE	JGCBEFB
957.	DIP	*Ropalomera pleuropunctata*	CCBBAAAA	LDB	CFABFB	CE	BCDF	BQE	AAAAA	DBKBDDAIC	CCECKAAEE	JGABEFA
958.	DIP	*Sepsis violacea*	CCCCAAAA	LDB	CFABFB	CE	BCEF	BQE	AAAAA	CCKBIDABC	CCECKAAEE	JXCBEFA
959.	DIP	*Sapromyza vulgaris*	CCBCAAAA	LDB	CFABFB	CE	BCEF	BQE	AAAAA	DDKBDBARC	CCECKAAEE	JG BEFA
960.	DIP	*Spaniocelyphus scutatus*	CCB AAAA	LDB	CFABFB	CE	BCEF	BQ	AAAAA	DDKBDBARC	CCECKAAEE	J FB
961.	DIP	*Opomyza florum*	CCB AAAA	LDB	CFABFB	CE	BCEF	BQE	AAAAA	CBKBCBAIC	CCECKAAEE	BBBEFA
962.	DIP	*Opomyza germationis**	AAFEADBA	MAA	BHCBBB	CE	BBFA	AMA	CJBEB	AAFBJDAAB	DBFBJAADA	DABDEDA
963.	DIP	*Clusiodies convergens*	CCBCAAAA	LDB	CFABFB	CE	CCBF	BQE	AAAAA	DCKBCCAAC	CCECKAAEE	JZCBEFA
964.	DIP	*Neoalticomerus seamansii**	AAFEADBA	MAA	CHCBBB	BE	BBBA	AMA	CJBEB	AAFCJDAAB	DCBAAAAAA	DUCBEDA
965.	DIP	*Agromyza* sp.	CCCCAAAA	LDB	CFABFB	CE	BCEF	BQE	AAAAA	DBKBCCARC	CCECKAAEE	JGCBEFA
966.	DIP	*Fergusonia tillyardi**	AAFEADBC	MAA	CHCBBB	BE	BBFA	AMA	CJPEB	AAFBJDAAB	DBBAAAAAA	DIABEDA
967.	DIP	*Periscelis annulipes*	CCCCAAAA	LDB	CFABFB	BE	BBBF	BQE	AAAAA	DBKBCCAIC	BCECKAAEE	JICBEFC
968.	DIP	*Neurochaeta inversa*	CBCBAAAA	LDB	CFABBB	CE	DBGF	BQE	AAAAA	CBFBDCAAC	CCECKAAEE	JGABEFA
969.	DIP	*Aulacigaster leucopeza**	AAFEADBC	OAA	BHCBBB	BE	DBDA	AMA	CJJEB	AAFCJDAAB	DCBAAAAAA	DICBEDA
970.	DIP	*Asteia concinna*	CCCCAAAA	LDB	CFABFB	CE	CBBF	BQE	AAAAA	DBFBDCAAC	CCECKAAEE	JI BEFB
971.	DIP	*Anthomyza gracilis*	CCCBAAAA	LDB	CFABFB		BCEF	B E	AAAAA	DBKBCBAIC	CCECKAAEE	JBBBEFA
972.	DIP	*Drosophila melanogaster*	CCBBAAAA	LDD	CFABFB	CE	BCDF	BQE	AAAAA	DBKBDCABC	CCECKAAEE	JVCBEFB
973.	DIP	*Mystacinobia zelandica*	CBDBAEAA	LAD	CFABFB	DB	BCBF	BQE	AAAAA	AAFCDCAAA	CCECKAAEE	JXABFFC
974.	DIP	*Camilla glabra*	CCBBAAAA	LDD	CFABFB	CE	BCBF	BQI	AAAAA	DBFBDCAAC	CCECKAAEE	CVCBEFB
975.	DIP	*Dichaeta caudata*	CCB AAAA	LDD	CFABFB	CE	BCCF	BQE	AAAAA	DBKBGCABC	CCECKAAEE	JQCBCFB
976.	DIP	*Ochthera mantis*	CCBCAAAA	LDD	CFABFB	CE	BCEF	BQC	AAAAA	DBKBBBABC	CCECKAAEE	JQCBCFB
977.	DIP	*Diastata nebulosa*	CCCBAAAA	LDB	CFABFB	BE	BCBF	BQE	AAAAA	CBKBDCAIC	DCECKAAEE	J BEFA
978.	DIP	*Curtonotum anus*	CCCBAAAA	LDB	CFABFB	CE	CBBF	BQE	AAAAA	CBKBDCAIC	CCECKAAEE	JU BFFB
979.	DIP	*Chlorops taeniopus*	CCBAAAAA	LCB	CFABFB	BE	CCCF	BQE	AAAAA	DBKBCCAIC	CCECKAAEE	JBBBEFA
980.	DIP	*Thaumatomyia glabra*	CCBCAAAA	LDB	CFABFB	CE	CCBF	BBE	AAAAA	DBKBDBARC	CCECKAAEE	JQCBEFA
981.	DIP	*Desmometopa latipes*	CCBCAAAA	LDB	CFABFB	CE	BCBF	BQE	AAAAA	DCKBDCAAC	CCECKAACE	JQCBFFA
982.	DIP	*Neomeconeurites chilensis*	CCBBAEAA	LDB	CFABFB	CE	EBDF	BQE	AAAAA	DBFBDBAAC	EAECKAABE	JPCBEFA
983.	DIP	*Tethinia illota*	CCB AAAA	LDB	CFABFB	CE	BC F	BQE	AAAAA	CCKBCBAIC	CCECKAAEE	JACBEFA
984.	DIP	*Canace macateei**	AAFEADBA	MAA	CHCBBB	BE	BBBA	AMA	CJBEB	AAFBJDAAB	DDBAAAAAA	D*CCGDA
985.	DIP	*Scatophaga furcata*	CCBBAAAA	LDB	CCHBFB	CE	BCBF	BQE	AAAAA	DCFBDBAAC	CCECLAAEO	CQBBEFB
986.	DIP	*Scopeuma stercoraria*	CBBBAAAA	LDB	CCHBFB	CE	ECEF	BQE	AAAAA	DBFBCBAAC	CCECLAAEO	CQBBEFB
987.	DIP	*Mormonomyia hirsuta**	AAFEADBA	MAA	CHCBFB	AA	AAAA	AMA	CJBEA	AAFBJDAAB	AAAAAAAAA	PXCEDDA
988.	DIP	*Gasterophilus intestinalis*	CBBBAAAA	LDD	CFABAA	AA	AAAA	BAA	AAAAA	AAAAAAAAA	DBEBJAAAA	QZEAFFA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
989.	DIP	_Gasterophilus nasalis_*	AAFEADBA	MAA	CHCBFB	CE	CBJA	ADA	CJBEB	AAFBJDAAB	DBBAA AAA	DSAEFDA
990.	DIP	_Anthomyia radicum_	CCBBAAAA	LDB	CCHBFB	BE	ECEF	BQE	AAAAA	D FBGBAAC	BCECLAAEO	COCBEFB
991.	DIP	_Hydrotaea dentipes_	CCBBAAAA	LDB	CCHBFB	CE	BCEF	BQ	AAAAA	DDFBGCAAC	CCECLAAEO	JGCBFFB
992.	DIP	_Hylemya alcathoe_*	AAFEADBA	MAA	BHCBFB	AA	AAAA	AMA	CJBEB	AAFBGCAAB	AAAAAAAAA	DJCDGDA
993.	DIP	_Fannia scalaris_	CCCBAAAA	LDB	CCHBFB	CE	BCDF	BQE	AAAAA	CBFBDCAAC	CCECLAAEO	JUCEDFA
994.	DIP	_Haematobia irritans_	CCCBAAAA	LDB	BCHBFB	BE	BCEF	BQE	AAAAA	DBFBDEAAH	BCECLAACO	CRBBEFB
995.	DIP	_Lyperosia minuta_	CCBBAAAA	LDB	CCHBFB	CE	BCEF	BQE	AAAAA	DBFBDCAAC	BCECLAAEO	CRCBFFB
996.	DIP	_Musca domestica_	CCBBAAAA	LDB	CCHBFB	CE	BCEF	BQE	AAAAA	DCFBDBAAC	CCECLAAEO	CUCBDFB
997.	DIP	_Musca domestica_*	AAFEADBA	AAA	BHCCFB	BE	AAAA	AMA	CJBEB	AAFCJDAAB	DBBAABAAA	DUCEDDA
998.	DIP	_Phaonia mirabilis_*	AAFEADBG	KAA	CHCBFB	AA	AAAA	AMA	CJBEA	DBFBJDAAB	EBBAAAAAA	DUCBDDA
999.	DIP	_Stomoxys calcitrans_	CCBBAAAA	LDB	CCHCFB	CE	ECDF	BQE	AAAAA	DBFBCBAAC	BCECLAACO	CRCBFFA
1000.	DIP	_Calliphora erythrocephala_	CCBBAAAA	LDB	CCHBFB	CE	ECEF	BQE	AAAAA	CCFBDEAAC	CCECLAAEO	CUCBEFA
1001.	DIP	_Calliphora erythrocephala_*	AAFEADBA	MAA	BHCBFB	CE	CBJA	AMA	CJBEB	AAFCJDAAB	CCBAAFAAA	DWCEFDA
1002.	DIP	_Cochliomyia macellaria_*	AAFEADBA	MAA	BHCBFB	BE	CBEA	AMA	CJBEB	AAFBJDAAB	DCBAABAAA	DWCEFDA
1003.	DIP	_Lucilia sericata_	CCBBAAAA	LDB	CCHBFB	CE	ECEF	BQE	AAAAA	DBFBDCAAC	CCECLAAEO	JWCBFFA
1004.	DIP	_Phormia regina_*	AAFEADBA	MAA	BHCBFB	BE	CBEA	AME	CJBEB	AAFCJDAAB	DCBAABAAA	DWCEFDA
1005.	DIP	_Sarcophaga haemorrhoidalis_	CCBBAAAA	LDB	CCHBFB	BE	BCDF	BQE	AAAAA	DDFBGBAAC	CCECLAAEO	JGCBEFA
1006.	DIP	_Wohlfhartia vigil_	CCBBAAAA	LDB	CCHBFB	BE	BCEF	BQ	AAAAA	DBFBDBAAC	CCECLAAEO	JGCBEFA
1007.	DIP	_Archytas analis_	CCBBAAAA	LDB	CCHBFB	CE	ECDF	BQE	AAAAA	DDFBGBAAC	BCECLAAEO	JGCBEFA
1008.	DIP	_Thelaira leucozona_	CCBBAAAA	LDB	CCHBFB	BE	BCDF	BQE	AAAAA	DBFBGBAAC	CCECLAAEO	JGCBEFA
1009.	DIP	_Cuterebra emasculator_	CCBBAAAA	LDB	CCCBFB	CE	EBDF	AGD	AAAAA	DBAAAAAAC	CCECKAADE	UGCBFFA
1010.	DIP	_Cephenomyia auribarbus_*	AAFEADBA	MAA	CHCBFB	CE	AAAA	AMA	CJBEB	AAFBJDAAB	DCBAABAAA	DSAEFDA
1011.	DIP	_Glossina palpialis_	CDCCAAAA	LDB	BCBBFB	CE	ECIK	BQF	AAAAA	DBFBCEAAH	BCECLAAFO	CRBBFFA
1012.	DIP	_Hippobosca maculata_	CDBBAAAC	LAB	BCBBFB	CE	EBDK	AQF	AAAAA	D FBFCAAH	BBECIAAFL	CRBBFFA
1013.	DIP	_Lychnia maura_	CCBBAAAC	EAB	BCBBFB	DE	EBDK	AQF	AAAAA	DBFBFDAAH	BBECIAAFL	CRBBFFA
1014.	DIP	_Melophagus ovinus_	CDBBAAAC	EAD	BCBBFB	DE	EBDK	AQF	AAAAA	DBFBFCAAH	BBECIAAFL	CRABFFA
1015.	DIP	_Olfersia ardeae_	CBBBAAAC	EAB	BCBBFB	CE	EBEK	AQF	AAAAA	DBFBDDAAH	CCECIAADL	CRABFFA
1016.	DIP	_Nycteribosca amboinensis_	CBBBAAAA	LAD	BCBBFB	DB	DBBK	AQF	AAAAA	DBFBFDAAH	DBECIAADL	CRABFFA
1017.	DIP	_Raymondia lobulata_	CBEBAAAA	LAA	BCBBFB	CE	ECDK	ABF	AAAAA	DCFBFDAAH	CCECIAADL	CRBBFFA
1018.	DIP	_Strebla vespertilionis_	CCBBAAAA	LAD	BCBBFB	CE	ECDK	AQF	AAAAA	DBFBFDAAH	DCECIAABL	CRABFFA
1019.	DIP	_Trichobius major_	CCBBAAAA	LAD	BCBBFB	CE	EBDK	A F	AAAAA	DBFBFDAAH	DBECIAABL	CRBBFFA
1020.	DIP	_Cyclopodia sykesi_	DDBBAAAC	EAE	BCBBFB	CE	BBIK	AQF	AAAAA	DBFBFCAAH	BBEBIAABL	CRABFFA
1021.	DIP	_Aecothea fenestralis_	CCBBAAAA	LDB	CGABFB	CE	BCEF	BQE	AAAAA	DDKBCBABC	CCECKAAEE	J BEFA
1022.	DIP	_Heleomyza serrata_*	AAFEADBA	MAA	CHCBBB	BE	BBFA	AMA	CJBEB	AAFBJDAAB	DBBAAAAAA	DUCBDDA
1023.	DIP	_Borborus equinus_	CCBCAAAA	LDB	CFABFB	CE	CCDF	B E	AAAAA	DCKBDBABC	CCECKAAEE	JUCBEFA
1024.	DIP	_Leptocera fontinalis_	CCBCAAAA	LDB	CFABFB	CE	CCCF	BQE	AAAAA	CBKCCCAIC	CCECKAAEE	JUCBEFA
1025.	DIP	_Sphaerocera curvipes_	CCBCAAAA	LDD	CFABFB	CE	BCDF	BQE	AAAAA	DBKCDCAIC	CCECKAAEE	JUCBEFA
1026.	DIP	_Gymnochyromya concolor_	CCBBAAAA	LDB	CFABFB	CE	CCBF	BQE	AAAAA	DBKBDDARC	CCECKAAEE	JA BEFA
1027.	DIP	_Cryptochaetum tuberculatum_*	AAFEADBA	MAA	BAABFA	AA	AAAA	CMJ	COBEA	AAFCJDAAA	ECFBJOADA	DSABFDA
1028.	DIP	_Braula coeca_	CBBCABAA	LAA	CFABBB	CE	DBBF	BA	AAAAA	CBHBJDRGC	CCECQAADE	K#ADFFB
1029.	TRI	_Agapetus fuscipes_	CBCBAAAA	BDB	CFABFB	CE	CBBF	BIN	AMBAA	BCJFHBFAC	DDEDDAABE	JGCBEFB
1030.	TRI	_Rhyacophila dorsalis_*	DAEBABAA	MCA	BAACCA	CE	DBGA	CKE	CFDBA	CDGEBCPBA	DDFCBKADM	EQCDBDA
1031.	TRI	_Rhyacophila septentrionis_	CBCBAAAA	BBB	CFABFB	CE	CCFF	BIN	AMBAA	BCJFHELAC	DCEDNAABE	JGCBEFC
1032.	TRI	_Hydrobiosis umbripennis_	BBCCAAAA	BDB	CFABFB	CE	CB F	BGD	AAAAA	BCJDGBFAC	CBEDDAABE	JGCBEFA
1033.	TRI	_Glossosoma_* sp.	CAEBABAA	MCA	BAABCA	CE	DBGA	CKE	CBLBA	BDKEBDA A	DDBAAKAAM	M*CCBDA
1034.	TRI	_Agraylea multipunctata_	CBC AAAA	BDB	CFABFB	CE	CBBF	BIN	AMBAA	BCJFHBFAC	DDEDNAABE	JGCBEFC
1035.	TRI	_Hydroptila_* sp.	CAEBABAA	DCA	BAACCA	CE	DBGA	CKE	CBLBA	BDKEBCAKA	DDFBJKADM	M*CBBDA
1036.	TRI	_Dolophiloides distinctus_	CBCCAAAA	BDB	CAABFB	CE	CBEF	BIN	AMBAA	BCFFCEAAC	DCEDDAABE	JGCBEFA

	order	taxon	mouthpart morphology data									dietary
			I	II	III	IV	V	VI	VII	VIII	IX	data
1037.	TRI	*Dolophiloides distinctus**	DAECABAA	MCA	BAABCA	BE	DBNA	CKE	CFDBA	BDKEBCAKA	CCFCJKADM	L*CCBDA
1038.	TRI	*Wormaldia occipitalis**	DAEBABAA	MCA	BAABCA	BE	DBNA	CKE	CMDBA	BDKEBCAKA	DCBAAKAAM	M*CCBDA
1039.	TRI	*Pseudostenopsyche sugens*	CCBBAAAA	BDB	CFABFB	CE	CBEF	BHE	AAAAA	GEC GBC	BDGDNFFBE	JGCBEFA
1040.	TRI	*Hydropsyche angustipennis*	CBBBAAAA	BAB	CFABFB	CE	CBEF	BIN	AMBAA	BCJFEEFAC	DCFDNIABE	JGCBEFC
1041.	TRI	*Hydropsyche pellucidula**	DAEBABAA	ACA	BAABCA	CE	DBGA	CKE	CBLBA	BDKEBCAKA	DDFCJKADM	L*CCBDA
1042.	TRI	*Macronemum ?zebratum**	DAEBABAA	ACA	BAABCA	CE	DBGA	CKE	CBLBA	BDKEBCAKA	DDBAAKAAM	L*CCBDA
1043.	TRI	*Plectrocnemia conspersa**	CAEBABAA	ACA	BAACCA	CE	DBGA	CKE	CFDBA	BDKEBBAJA	CBFBQKACM	EPCEBDA
1044.	TRI	*Polycentropus flavomaculatus*	CBC AAAA	BAB	CFABFB	CE	CBEF	BIN	AMBAA	BCJFEELAC	DDFDNIABE	JGCBEFC
1045.	TRI	*Dipseudopsis africana*	CBBAAAAA	BAB	CEABFA	CE	CCBA	BBL	AMBAA	BCGFEEEAI	DCEDNAABJ	KGCBEFC
1046.	TRI	*Ecnomus tenellus*	BBCCAAAA	BAB	CFABFB	CE	CBEF	BIN	AMBAA	BCJFEEFAC	DBFDNIABE	JGCBEFA
1047.	TRI	*Tinodes waeneri*	BBCCAAAA	BAB	CFABFB	CE	CBBF	BIN	AMBAA	BCJFEEFAC	DCEDNAABE	JGCBEFA
1048.	TRI	*Philostomis postica**	DAEBABAA	MCA	BAABCB	CE	CBGA	CKE	CBDBA	BDKEBDAKA	DDFCJKADM	E&CDBDA
1049.	TRI	*Phryganea cinera**	DAEBABAA	MCA	CAABCA	CE	DBGA	CKE	CBDBA	BDKEBCAKA	D FCJKADM	E&CDBDA
1050.	TRI	*Phryganea striata*	CBBBAAAA	BDB	CFABFB	CE	DBGF	BIN	AMBAA	BCJECEFAC	DCEDNAACE	JGCBEFC
1051.	TRI	*Phryganopsyche latipennis**	CBBBABAA	OEA	BFABCA	CE	BBFA	CKE	CBDBA	CCHEBCQHA	CCFCDKACM	E&CCBDA
1052.	TRI	*Brachycentrus subaubilus*	CBBCAAAA	BAB	CFABFB	CE	CBEF	BIN	AAAAA	BCJDGCFAC	DCEDDAABE	JGCBEFC
1053.	TRI	*Philansus plebius**	CAE ABAA	ACA	CAABCA	CE	DBNA	CKE	CBLBA	BDKDBDAKA	DCGBJKFDM	EPCDBDA
1054.	TRI	*Tasimia natasia*	BBCCAAAA	BAB	CFABFA	CE	DBGF	BIN	AMBAA	CBJECEFAC	CDEDDAABE	JGCBEFC
1055.	TRI	*Anabolia furcata*	CBCCAAAA	BDB	CFABFB	CE	DCBF	BIN	AAAAA	BCJFCEFAC	DCEDDAACE	JGCBEFA
1056.	TRI	*Anabolia furcata**	CAEBABAA	MCA	CAABCB	CE	DBGF	CKE	CBDBA	CDKEBDA A	CDFCJKADM	EVCDBDA
1057.	TRI	*Drusus trifidus**	CAECABAA	MCA	CAABCA	CE	CBGA	CKE	CBLBA	BDKEBDAKA	CDFCJKADM	EVCDBDA
1058.	TRI	*Dicosmoecus** sp.	CAECABAA	MCA	CAABCA	CE	DBGA	CKE	CB BA	BDKEBCA A	CDFCJKADM	E*CDBDA
1059.	TRI	*Limnephilus flavicornis**	CAEBABAA	MCA	CAABCA	CE	CBCA	CKE	CDLBA	BDKEBCAJA	DCFCBKADM	M*CCBDA
1060.	TRI	*Limnephilus lunatus*	CBBCAAAA	BDB	CFABFB	CE	DCBF	BIN	AAAAA	BCJDCEFAC	DDEDNAACE	JGCBEFA
1061.	TRI	*Stenophylax permistus**	CAECABAA	MCA	BAABCA	CE	DBCA	CKE	CDLBA	BDKEBDAJA	DDFDBKADM	MVCDBDA
1062.	TRI	*Goera pilosa*	BBBCAAAA	BAB	CFABFB	CE	DCBF	BIN	AAAAA	BCJDCCFAC	DCEDNAABE	JGCBEFA
1063.	TRI	*Goera pilosa**	CAECABAA	MCA	CAABCA	CE	DBGA	CKE	CBLBA	BDKEBDAJA	DDFCBKADM	M*CCBDA
1064.	TRI	*Thremma anomalum**	CAEBABAA	MCA	BAACCA	CE	CBCA	BKN	CBFBA	BDGDJDJIA	CCFCBKADM	M*BCBDA
1065.	TRI	*Lepidostoma hirtum**	CAECABAA	MCA	BAABCA	BE	DBGA	CKE	CBLBA	BDKEBCAJA	D FCBKADM	E*CCBDA
1066.	TRI	*Zelandopsyche ingens*	BBCCAAAA	BAB	CFABFB	CE	DBBF	BIN	AAAAA	CBJDGBFAC	CBFDDOIFE	JGCBBFC
1067.	TRI	*Taskiropsyche lacustris*	BBCBAAAA	BAB	CFABFB	CE	DBEF	BIN	AAAAA	CCJEBBJAC	DBEDDAABE	JGCBEFC
1068.	TRI	*Plectrotarsus gravenhorstii*	ECBBAAAA	BAB	CFABFB	CE	EBDF	BIN	AMBAA	CCJDCBFAC	CCFDDAABE	JGCBEFC
1069.	TRI	*Beraea maurus*	CBB AAAA	BAB	CFABFB	CE	DBBF	BIN	AMBAA	BCJFCEFAC	DCEDDAABE	JGCBEFC
1070.	TRI	*Crunoecia irrorata*	CBBCAAAA	BAB	CFABFB	CE	DBBF	BIN	AAAAA	BCJBGCFAC	DCEDDAAFE	JGCBEFC
1071.	TRI	*Notidobia ciliaris*	CBBCAAAA	BAB	CFABFB	CE	DBBF	BIN	AMBAA	BCGBGCFCC	DDEDDAABE	JGCBEFC
1072.	TRI	*Notidobia ciliaris**	CAEBABAA	ACA	BAABCA	BE	CBGA	CKE	CBLBA	CDKEBCAMA	DCFDBKADM	EVCDBDA
1073.	TRI	*Sericostoma personatum*	CBBCAAAA	BAB	CFABFB	DE	DBBF	BIN	AMBAA	CCGB DFBC	DCEDBAABE	JGCBEFC
1074.	TRI	*Tamasia variegata*	BBCCAAAA	BAB	CFABFB	CE	DBBF	BIN	AAAAA	BBJEECFAC	DBEDDAAFE	JGCBEFC
1075.	TRI	*Pycnocentria sylvestris**	CAEBABAA	MCA	BAABCA	CE	BBGA	CKE	CBLBA	BCKEBCAMA	DCFBBKADM	EZCDBDA
1076.	TRI	*Zelolessica cheira**	CAEBABAA	MCA	BAABCA	CE	BBGA	CKE	CBLBA	BDKEBCAMA	DCFBBKADM	EVCDBDA
1077.	TRI	*Molanna angustata*	CBB AAAA	BAB	CFABFB	CE	CBBF	BIN	AMBAA	BCJFCEFAC	DCEDDAABE	JGCBEFA
1078.	TRI	*Molanna angustata**	DAEBABAA	MCA	CAABCA	BE	DBBA	CKE	CFDBA	BDKDBCAMA	DCFBJKADM	M&CDBDA
1079.	TRI	*Odontocerum albicorne*	CBCCAAAA	BAB	CFABFB	CE	CBBF	BIN	AMBAA	BCJFCEFAC	DCEDDAABE	JGCBEFA
1080.	TRI	*Odontocerum albicorne**	CAECABAA	MCA	CAACCA	BE	DBGA	CKE	CBDBA	BDKEBCAMA	D FCJKADM	M&CDBDA
1081.	TRI	*Psilotreta** sp.	DAEBABAA	MCA	CAABCA	BE	DBGA	CKE	CBDBA	BDKEBCAKA	CDFBJKADM	MVCDBDA
1082.	TRI	*Atriplectides dubius**	DABBABAA	MAD	BAABCA	DB	CBBA	CKE	CLDBA	BCKDBDAJA	DCFBJKADM	M*CCBDA
1083.	TRI	*Tasmanthrus angustipennis*	BBCCAAAA	BAB	CFABFB	BE	CBEF	BIN	AMBAA	BCJEHCFAC	CBEDDAAFE	JGCBEFC
1084.	TRI	*Helicopsyche borealis**	CAEBABAA	MCA	CAABCA	CE	DBGA	CKE	CB BA	CDKEBCAJA	DCFBJKADM	M*CCBDA
1085.	TRI	*Heteroplectron americanum**	CAEBABAA	ACA	CAABCA	CE	DBGA	CKE	CBLBA	BDKEBCAJA	DCFBJKADM	EVCDBDA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
1086.	TRI	*Athripsodes cinera*	CBBCAAAA	BAB	CFABFB	CE	CCBF	BIN	AMBAA	BCJFCEFAC	DCEDDAABE	JGCBEFC
1087.	TRI	*Mystacides sepulchralis*	CBB AAAA	BAB	CFABFB	CE	CCEF	BIN	AAAAA	CCJFCEFAC	DCEDNAABE	E&CDEFA
1088.	LEP	*Heterobathmia pseuderiacrania*	CACCAAAA	CCD	CAACFA	DB	CBJA	CQK	CBDBA	BCGFCEJCA	DDGDDBICA	EHACEFA
1089.	LEP	*Heterobathmia pseuderiacrania**	CAEAABBA	NEA	BAABCA	DB	DBBM	CKN	CBLBA	CDJDBDJAA	CCFBQKADM	EEADEDA
1090.	LEP	*Micropteryx calthella*	BABCAAAA	CCB	CAACFA	DB	CBJA	CQK	CCCBA	CDGFBEIRA	DDGCDBFCA	EHACEFA
1091.	LEP	*Micropteryx calthella**	CAECABBA	KAA	BAABCA	DB	DBBA	CJE	CFDBA	BCGDBCG A	DBECBAACA	EEBDEDA
1092.	LEP	*Mnemonica auricyanea*	CACCAAAA	CCD	CAABFA	DB	CBDA	CQK	CBEBA	CDGGBEGBA	DCECCAABA	EHBCEFA
1093.	LEP	*Palaeomicroides fasciatella*	CABCAAAA	DCB	CAACFA	DB	CBJA	CQK	CCEBA	BDGFBEICA	DCEDDAACA	EH CEFA
1094.	LEP	*Sabatinca auruncella*	CABCAAAA	BCB	CAACFA	DB	CBJA	CQK	CCEBA	BCGF EICA	DCEDDAACA	EMACEFA
1095.	LEP	*Sabatinca barbarica**	CAECABBA	KEA	CAACCA	DB	DBGA	CJE	CFLBA	BCGDBCPCA	DBEDBAADA	EEBDEDA
1096.	LEP	*Agathiphaga vitiensis*	CAC AAAA	DAB	CAACFB	DB	DBFA	CQC	CBBBA	BCGFCBKCA	DCEEDAABA	I FA
1097.	LEP	*Agathiphaga vitiensis**	CAECADBA	MAA	BAABFA	AA	DBGA	CKC	CRDBA	BCJCJDBAA	DCFBJQADM	ECADEDA
1098.	LEP	*Eriocrania sangi**	CAEAABBA	KCA	BAABCA	CE	CBGA	CHC	CFDBA	BCJCJDIAA	DBE AA A	EEBDEDA
1099.	LEP	*Eriocrania semipurpurella*	CCBCAAAA	CCD	CEABFB	CE	CBDL	AAC	CDBBA	BCGFCEE I	DCEDDAAFJ	KICBEFA
1100.	LEP	*Lophocorona pediasia*	CCCCAAAA	CAB	CEABFB	CD	DEEL	AAE	ABBAA	BCJECEEAI	DCEDDAABJ	KG BEFA
1101.	LEP	*Archepiolus schmidi*	CCCCAAAA	DAB	CEABFB	CB	CBEL	AAC	CBBBA	CDJFCEEAI	DCEDDAAFJ	K FA
1102.	LEP	*Neopseustis meyricki*	CCBCAAAA	DAB	CEABFB	CE	CBJL	AQE	ABBAA	BCJFGEEAI	DCEDOAAFJ	KG BEFA
1103.	LEP	*Mnesarchaea loxoscia*	CCCCAAAA	CAB	CEABFB	CD	CEEL	AAE	ABBAA	CCJDGCEAI	DCEDCAACJ	KG BEFA
1104.	LEP	*Neotheora chiloides*	BCCAAEAA	CAB	CEABFA	CA	AAAA	AAA	AAAAA	BCJCJDEAI	DCEDOAABJ	K FEFB
1105.	LEP	*Azaleodes fuscipes*	BDCCAEAA	BAB	CEABFB	CE	BELL	AAE	CBBAA	BCJFBEEAI	CBEDOAABJ	K BEFC
1106.	LEP	*Afrotheora thermodes*	BACCAEAA	BAB	CGABAA	CE	BEEA	DAA	AAAAA	AAFDJDAAA	CBECOAACA	QZEAEFC
1107.	LEP	*Hepialus* sp.	BABBAAAA	B B	CEABAA	CE	CBBA	AA	AAAAA	BCJBJDBAI	DCECOAACA	QZEAEFA
1108.	LEP	*Hepialus humuli**	CAECABBA	KEA	BAABFA	CE	CB M	CKC	CB BA	CCHDBDFAA	DCFBKKACM	EHBDGDA
1109.	LEP	*Stenopis thule*	BACCAAAA	B B	CGABAA	CE	CBBA	DAE	AAAAA	BCJDBDBAA	DDECOAACA	QZEAEFA
1110.	LEP	*Ectoedemia heinrichi**	CAECABBA	MCA	BAABFA	DB	CBIM	CKE	CBDBA	BCGDBDBBA	DCEDLAABA	EEADEDA
1111.	LEP	*Nepticula malella**	CAECABBA	MCA	BAABFA	DB	CBIM	CKC	CBDBA	BCGDFDGRA	DDECLAABA	EEADEDA
1112.	LEP	*Opostega** sp.	CAEBAABA	KAA	BAABFA	DB	CCCM	CKG	CBLBA	BDGDBDGKA	DBFCJKABM	EEADEDA
1113.	LEP	*Tischeria marginea**	CAEAABBA	NEA	BAABDA	BE	DBIM	CKC	CBDBA	BCJCCDGAA	CDFBBKADM	EEADEDA
1114.	LEP	*Paraclemensia acerifoliella**	CAE ABBA	NEA	BAABFA	CE	DBBM	CKC	CBDBA	CCJDBDBAA	CCECLAACA	EEADEDA
1115.	LEP	*Tegeticula yuccasella*	BDBCAAAA	BAB	CEABFB	CE	B L	AAC	AAAAA	CDJF EEAI	DCEEDAABJ	KGABEFB
1116.	LEP	*Prodoxus quinquepunctella**	CAEBABBA	NDA	BAABFA	CB	DBGN	CKC	CBDBA	CDJDBDHAA	DDECBAADM	EJADEDA
1117.	LEP	*Coptodisca splendoriferella**	CAEBABBA	KCA	BAABFA	CE	CBMM	CK	CBDBA	BCJCBDGAA	CCFCLKABM	EEBDEDA
1118.	LEP	*Lindera tessellatella**	CAECABBA	NAA	BAABFA	CE	CBGM	CKG	CRDBA	BDJCBDJAA	DCFCLKACM	EQCDDDA
1119.	LEP	*Tinea pellionella**	CAE ABBA	NEA	BAABFA	CE	DBGM	CKG	CRDBA	BBJDBDIAA	DCFBLKACM	E$ADFDA
1120.	LEP	*Thrydopteryx ephemeraeformis**	CAE ABBA	NEA	CAABFA	DB	DBCM	CK	CRDBA	CCJCBDIAA	DCFBLKACM	EECDEDA
1121.	LEP	*Eriocottis fuscanella*	CDBAAAAA	CCB	CEABFB	CE	BBLL	AAC	AAAAA	BCJECBEAI	CBEDOAABJ	K BEFC
1122.	LEP	*Oschenheimeria vacculella*	CDBAAAAA	BCB	CEABFB	CE	BBLL	AAC	AAAAA	BDJCCDEAI	CBEDOAACJ	K BEFC
1123.	LEP	*Phyllocnistis suffusella**	CAE ABBA	NCA	BAABFA	CE	DBNM	CKE	CMDBA	CBFBICAAA	CBBAAKAAM	EIABEDA
1124.	LEP	*Gracillaria stigmatella**	CAEBABBA	NAA	BAABFA	CE	DBIM	CKG	CRDBA	CBJBJDBAA	CBEBJKADM	EEADEDA
1125.	LEP	*Bdellia somnulentella**	CAECABBA	MEA	BAABFA	CE	DBGM	CKE	CRDBA	CDJDBDIAA	CDFBLKACM	EEADEDA
1126.	LEP	*Paraleucoptera sinuella**	CAECABBA	MEA	BAABFA	BE	DBNM	CKE	CBDBA	CDJCJDIAA	DCEBLKABM	EEBDEDA
1127.	LEP	*Depressaria heracliana**	CAECABBA	NEA	BAABFA	CE	DBBM	CKE	CRDBA	CDJDBDBAA	CBFCLKACM	EEADEDA
1128.	LEP	*Oecophora bractella*	BDC AAAA	BAB	CEABFB	DE	CBLL	AAC	AAAAA	BCJEGBEAI	CBEDOAAFJ	KG BEFA
1129.	LEP	*Ethmia longimaculella**	CAECABBA	NEA	CAABFA	CE	DBCM	CKE	CRDBA	CCJCBDJAA	CCFBLKACM	EEADEDA
1130.	LEP	*Eriogenes mesogypsa*	CDCCAAAA	BAB	CEABFB	CE	CBLL	AAC	AAAAA	BCJEGCEAI	CBEDOAABJ	KGCBEFA
1131.	LEP	*Stenoma schlaegeri**	CAECABBA	NEA	CAABFA	CE	DBCM	CKE	CRLBA	CDJDBDBAA	DBFCLKACM	EEADEDA
1132.	LEP	*Coleophora veronioella**	CAECABBA	NEA	BAABFA	CE	DBBM	CK	CRDBA	CDJDJDSAA	CCFBLKA M	EEADEDA
1133.	LEP	*Valentinia glandulella**	CAECABBA	NEA	BAABFA	CE	DBGM	CKE	CRDBA	BDFCBCAAA	CCFCLKACM	ECADEDA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
1134.	LEP	_Elachista madarella_	BDBCAAAA	BAB	CEABFB	DE	CBLL	AAC	AAAAA	DCJBGDEAI	CBEDOAABJ	KGCBEFA
1135.	LEP	_Ithome concolorella_*	CAEBABBA	NEA	BAABDA	CE	BBCA	CKE	CBDBA	BCHCCDNQA	DCFCLKACM	EDBDEDA
1136.	LEP	_Aristotlea hermanella_*	CAECABBA	NEA	BAABFA	CE	CBCM	CAC	CRDBA	CDJDBDJAA	DDFBLKACM	EEADEDA
1137.	LEP	_Gnorimoschema gallasolidagnis_*	CAECABBA	NEA	BAABFA	CE	DBCM	CKE	CRDBA	CDJDBDJAA	CDFCLKACM	EEADEDA
1138.	LEP	_Scythris epilobiella_*	CAEBABBA	NEA	BAABFA	CE	DBGM	CK	CRDBA	BDFDBCAAA	CCFBLKACM	EEADEDA
1139.	LEP	_Cosmopteryx zieglerella_	BDC AAAA	BAB	CEABFB	DB	CBLL	AQC	AAAAA	CCJEGBEAI	CBEDOAAFJ	EG BEFA
1140.	LEP	_Carposina fernaldana_*	CAEBABBA	AEA	BAABFA	CE	DBCM	CK	CRDBA	BDJDBCJAA	DCFBLKACM	EEADEDA
1141.	LEP	_Epimerina albapunctella_*	CAECABBA	NEA	CAABFA	CE	DBGM	CK	CRDBA	CDJCBDGAA	CCFBLKACM	EEADEDA
1142.	LEP	_Anthophila pariana_*	CAEAABBA	NEA	BAABFA	DB	DBBM	CK	CRDBA	CBFDBCAAA	CBFBLKACM	EEBDEDA
1143.	LEP	_Atteva aurea_*	CAECABBA	NEA	CAABFA	CE	DBCM	CKE	CRDBA	BDJCBCGAA	DCFBLKACM	EEADEDA
1144.	LEP	_Sanninoidea_ sp.	BDBCAAAA	BCB	CEABFB	DE	CBLL	AAC	AAAAA	BCJDGDEAI	CBEDOAACJ	KG BEFA
1145.	LEP	_Podosesia syringae_*	CAE ABBA	NEA	BAABFA	CE	BGM	CKE	CRDBA	CCJBJDJAA	CCFBLKACM	EJBDEDA
1146.	LEP	_Imma_ sp.	BDBAAAAA	BAB	CEABFB	CE	BBLL	AAC	AAAAA	BCBAAAEAA	CBEDOAABJ	K BEFC
1147.	LEP	_Cossus cossus_*	CAECABBA	MEA	CAABFA	BE	DBBM	CKE	CRDBA	CCJCBDJAA	CDFCLKACM	EJCDEDA
1148.	LEP	_Prinoxystus robinae_*	CAEBABBA	KEA	CAABFA	CE	DBGM	CKE	CRDBA	BDJDBDJAA	CCFBLKADM	EKCDEDA
1149.	LEP	_Zeuzera pyrina_*	CAECABBA	NEA	CAABFA	DB	CBGM	CKE	CDDBA	CDJCBDJAA	CDFCLKACM	RKCDEFA
1150.	LEP	_Archips cerasivorana_*	CAEBABBA	NEA	BAABFA	DB	CBGM	CKC	CRDBA	BDJEBCJAA	CDFCLKACM	EEADEDA
1151.	LEP	_Choristoneura argyrospila_*	CAEBABBA	NEA	BAABFA	CE	BGM	CKC	CRDBA	DDJCBCJAA	CDFBLKACM	EEADEDA
1152.	LEP	_Choristoneura fumiferana_	CDCAAAAA	GAB	CEABFB	DB	DBLL	AAO	AAAAA	BCJDGDEAI	DBEDOAABJ	QZEAEFA
1153.	LEP	_Cydia pomonella_*	CAEBABBA	NEA	BAABFA	CE	DBGM	CKM	CRDBA	BDJCBDJAA	CCFCLKACM	EFADEDA
1154.	LEP	_Stenodes alternana_*	CAECABBA	NDA	CAABFA	CE	BBBM	CKE	BRDBA	BCJDBCJAA	CBFCLKACM	EDADEDA
1155.	LEP	_Harrisina americana_*	CAEAABBA	OEA	CAABFA	CE	BGM	CKC	CRDBA	CDJEBCJAA	D FBLKACM	EEADEDA
1156.	LEP	_Somatobrachys infuscata_	CBCAAEAA	EAB	CGABAA	AB	CAAA	DAA	DAAAA	AABAAABAA	AAAAAAAAA	QZEAEFA
1157.	LEP	_Lagoa crispata_*	CAE ABBA	NEA	CAABFA	B	CBCM	CKC	CRDBA	BDJDBDJAA	DDFCLKABM	EECDEDA
1158.	LEP	_Epipomponia elongata_	CBBCAEAA	EAB	CGABAA	CE	AAAA	DAA	DAAAA	BBBAAAAAA	AAAAAAAAA	QZEAEFB
1159.	LEP	_Castnia icarus_	BDCBAEAA	GAB	CEABFB	CE	DCBL	AAL	AAAAA	CCJBJDEAI	DCEDOAABJ	KGCBEFA
1160.	LEP	_Epargyreus clarus_	BDBBAEAA	GAB	CEABFB	DE	DBJL	AAL	AAAAA	CCJBJDEAI	DCEDNAACJ	KGCBEFA
1161.	LEP	_Panoquina ocola_	BDBBAEAA	GAB	CEABFB	DE	DBBL	AAL	AAAAA	CCJBJDEAI	DCEDOACCJ	KGCBEFA
1162.	LEP	_Quinta cannae_	BDBBAAAA	GAB	CEABFB	DE	DBBL	AAL	AAAAA	CDJBJDEAI	DCEDOAA J	KGCBEFA
1163.	LEP	_Tagiades flesus_	BDBBAAAA	GAB	CEABFB	DE	DBLL	AAL	AAAAA	CCJBJDEAI	DCEDOAACJ	K FA
1164.	LEP	_Urbanus dorantes_	BDBBAAAA	GAB	CEABFB	DE	DBLL	AAL	AAAAA	CCJBJDEAI	DCEDOAACJ	KGBBEFA
1165.	LEP	_Megathymus yuccae_	BDBBAEAA	GAB	CEABFB	CE	DBGL	AAL	AAAAA	CCJCJDEAI	DCEDOAABJ	K/ABDFA
1166.	LEP	_Battus philenor_	BDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	AAAAA	CCEAAAECI	DBEDOAABJ	KGCBEFA
1167.	LEP	_Papilio demoleus_	BDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	AAAAA	CCEAAAECI	EBEDOAACJ	KGCBEFA
1168.	LEP	_Parides iphidanus_	CDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	AAAAA	CCEAAAECI	DBEDOAABJ	KGCBEFA
1169.	LEP	_Teinopalpus imperalis_	CDBAAAAA	GAB	CEABFB	DE	DBBL	AAL	AAAAA	CEAAAECI	BEDOAABJ	KG BEFA
1170.	LEP	_Eurema deva_	CDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	ABBAA	CDJCJDEAI	CBEDOAABJ	K/ABDFA
1171.	LEP	_Pieris brassicae_	BDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	ABBAA	CDJCJDEAI	DBEDOAABJ	KGCBEFA
1172.	LEP	_Celastrina argiolus_	CDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	AAAAA	CCEAAAECI	DBEDOAABJ	K&CBEFA
1173.	LEP	_Lycaena helloides_	CDCAAEAA	GAB	CEABFB	BE	DBLL	AAL	AAAAA	CCEAAAECI	DBEDOAABJ	KEABEFA
1174.	LEP	_Apodemia palmeri_	CDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	AAAAA	CCBAAAEAI	DBEDOAA J	KGABEFA
1175.	LEP	_Lasaia agesilus_	CDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	AAAAA	CCBAAAEAI	DBEDOAABJ	KGABEFA
1176.	LEP	_Danaus archippus_	BDCAAEAA	GAB	CEABFB	CE	DBLL	AAL	ABBAA	CCBAAAEAI	DBEDOAACJ	KGABEFA
1177.	LEP	_Anartia fatima_	BDCAAAAE	GAB	CEABFB	CE	CBLL	AA	AAAAA	CDJBJDEAA	DBEDFKA J	KGBBEFA
1178.	LEP	_Basilarcha archippus_*	CAEBABBA	OEA	CAABFA	CE	BGM	CKG	CRDBA	BDJCBCJAA	CDFBBKACM	EEBDEDA
1179.	LEP	_Calinaga buddha_	CDCAAEAE	GAB	CEABFB	CE	DBLL	AAL	AAAAA	CCJBJDEAI	DBEDOAA J	KG BEFA
1180.	LEP	_Heliconius charitonia_	BDCAAEAE	GAB	CEABFB	CE	DBLL	AAL	AAAAA	CCJBJDEAI	DBEDOAA J	KHBCEFA
1181.	LEP	_Vanessa cardui_	BDCAAEAE	GAB	CEABFB	CE	DBLL	AAB	AAAAA	CCJBJDEAI	DBEDOAA J	KGCBEFA
1182.	LEP	_Vanessa cardui_*	CAECABBA	NEA	BAABFA	E	DBCM	CKC	CRDBA	BCJDBDJAA	DCFBLKACM	EECDEDA

	order	taxon	mouthpart morphology data									dietary data
			I	II	III	IV	V	VI	VII	VIII	IX	
1183.	LEP	Platyptilia carduidactyla*	CAEBABBA	KEA	CAABFA	CE	BGM	CKG	CRDBA	CDJDBCJAA	CDFBLKACM	EEADEDA
1184.	LEP	Neobansia fuliginea	CDCAAAAA	GAB	CEABFB	DE	CBLL	AAI	AAAAA	BCJDGDEAI	DBEDFAACJ	KG BEFA
1185.	LEP	Acroia grisella*	CAEBABBA	KAA	BAABFA	CE	CBBN	CKC	CRDBA	CDJCBDJAA	CDFDLKACM	EUCDDDA
1186.	LEP	Bissetia steniellus	CDCCAAAA	BCB	CEABFB	DB	DBLL	AAI	AAAAA	BCJEGCEAI	DBEDFAABJ	KG BEFA
1187.	LEP	Chilo tumidicostalis	CDCAAAAA	BCB	CEABFB	DB	BLL	AAI	AAAAA	BCJEDCEAI	DBEDFAABJ	KG BEFA
1188.	LEP	Chilotraea infuscatellus	CDCAAAAA	BCB	CEABFB	DB	DBLL	AAI	AAAAA	BCJECCEAI	DBEDFAABJ	KG BEFA
1189.	LEP	Galleria mellonella*	CAEBABBA	KEA	BAABFA	CE	DBGM	CKC	CRDBA	BDHCBDJAA	CDFBBKACM	E*ADFDA
1190.	LEP	Haritala ruralis	CDCAAAAA	GCB	CEABFB	CE	DBLL	AAE	AABBA	CDJEGCEAI	CCEDFAABJ	K FA
1191.	LEP	Homoeosoma electellum*	CAEBABBA	EA	BAABFA	CE	DBCM	CKC	CRDAA	B JDBDJAA	CDFCLKACM	EBBDEDA
1192.	LEP	Scirpophaga nivella	CCCAAAAA	BCB	CEABFB	DB	DBLL	AAG	AABBA	BDGECCERI	CCFDFBABJ	KG BEFA
1193.	LEP	Euthyratira* sp.	CAEBABAA	NEA	CAABFA	DB	DBGM	CK	CRDBA	JCJDJAA	CCFCBKACM	EEADEDA
1194.	LEP	Drepana arculata*	CAEBABAA	KEA	CAABFA	DB	DBCM	CKC	CRDBA	JCJDJAA	CCFBLKACM	EEBDEDA
1195.	LEP	Ourapteryx sambucaria*	CAEBABAA	KEA	CAABFA	CE	DBCM	CKC	CRDBA	JCJDJAA	CCFBLKACM	EEBDEDA
1196.	LEP	Lacosoma chiridota*	CAEBABAA	KEA	CAABFA	CE	DBCM	CKC	CRDBA	CDJCJDJAA	CCFBLKACM	EEADEDA
1197.	LEP	Bombyx mori*	CAEBABBA	NEA	CAABFA	CE	CBCM	CKC	CRDBA	BDJCJDJAA	DCFCLKACM	EEADEDA
1198.	LEP	Malacosoma americana*	CAEBABBA	KEA	CAABFA	DB	CBCM	CKC	CRDBA	BCJCJDJAA	CCFBJKADM	EEBDEDA
1199.	LEP	Malacosoma neustria	CACAAAAA	EAB	CGABAB	CE	DBBA	DQE	AAAAA	CDJBJDAAA	DBEDFAACM	QZEAEFA
1200.	LEP	Carthaea saturnoides	BDCBAAAA	EAB	CEABFA	CE	BBLL	AQE	AAAAA	BCJDECEAI	DBEDDAABJ	KGDBEFC
1201.	LEP	Automeris io*	CAEBABAA	KEA	CAABFA	DB	DBCM	CKE	CRDBA	CDJCJDJAA	DCFBLKADM	EECDEDA
1202.	LEP	Dryocampa rubicunda	BACBAAAA	BAB	CGABFA	CB	DBLA	DQE	ABBAA	BBFBGDAAA	DBEBFAABJ	QZEADFA
1203.	LEP	Eacles imperalis	BCCAAEAA	EAB	CEABFB	CE	DBLL	AQE	AAAAA	CBJBJDEAI	DBECFAACJ	QZEAEFA
1204.	LEP	Telea polyphemus*	CAEBABBA	NEA	CAABFA	DB	CBCM	CKE	ARDAA	BDJDBDJAA	CDFCLKACM	EECDEDA
1205.	LEP	Acherontia atropos*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKE	CRDBA	BCFCBDAAA	DBFCBKADM	EEBDEDA
1206.	LEP	Agrius convolvuli	CDCAAAAA	BAB	CEABFB	DE	DBLL	AQL	ABBAA	CCJCCDEAI	DBEEFAABJ	KECDEFA
1207.	LEP	Dilina tiliae	BDCAAAAA	BAB	CEABFB	CE	DBLL	AQL	ABBAA	CCJBJDEAI	DBEDFAA J	K FC
1208.	LEP	Dilina tiliae*	CAECABAA	MEA	CAABFA	CE	CBCM	CKE	CRDBA	BCJCJDJAA	CCFBLKADM	EE DA
1209.	LEP	Dolba hylocus*	CAEBABAA	KEA	CAABFA	DB	CBCM	CKE	CRDBA	BDJCJDJAA	CDFBLKADM	EEADEDA
1210.	LEP	Manduca sexta	BDCAAAAA	BAB	CEABFB	CE	DBLL	AQL	ABBAA	CCJBJDEAI	DBEDFAACJ	KGCBEFC
1211.	LEP	Manduca sexta*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKE	CRDBA	BDJDBDJAA	CCFCBKACM	EEBDEDA
1212.	LEP	Schizura concinna*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKE	CRDBA	CDGCBDJBA	CCFBLKACM	EFBDEDA
1213.	LEP	Orgyia leucostigma*	CAEBABAA	NEA	CAABFA	DE	DBCM	CKC	CRDBA	CDJCBDJAA	CCFBLKACM	EECDEDA
1214.	LEP	Estigmene acrea*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKC	CRDBA	BDJCBDJAA	DDFBLKABM	EECDEDA
1215.	LEP	Euchaetes egle*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKC	CRDBA	BDJCBDJAA	CDFDLKACM	EEADEDA
1216.	LEP	Hyphantria cunea	CDCAAAAA	FAB	CEABFB	CE	DBLL	AQL	ABBAA	CCJBJDEAI	DBEDFAABJ	QZEAEFA
1217.	LEP	Pyrrharctia isabella*	CAEAABAA	NEA	CAABFA		CBCM	CKC	CRDBA	BDJCBDJAA	CDFBLKACM	EECDEDA
1218.	LEP	Ctenuchia sp.	BD AAAA	EAB	CEABFB	DE	DBLL	AQL	AAAAA	CCJBJDEAI	DBEDFAABJ	KGBBEFA
1219.	LEP	Calyptra eustrigata	BDCBAAAA	EAB	CBCBFB	CE	CB I	AAE	AAAAA	CDBAAADAF	DBEDFAABI	ARBBFFA
1220.	LEP	Catocala sp.	BDCBAAAA	CAB	CEABFB	CE	CBLL	AQE	AAAAA	BCJBGDEAI	DBEDFAABJ	EF BEFA
1221.	LEP	Catocala* sp.	CAEBABAA	NEA	CAABFA	DB	DBCM	CK	CRDBA	BDJCBDJAA	CDFDLKACM	EEADEDA
1222.	LEP	Lacinipolia renigera*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKC	CRDBA	BDJCBDJAA	CDFDBKADM	EECDEDA
1223.	LEP	Othreis materna	CDCAAAAA	CAB	CBCBFB	CE	CBBI	AAE	AAAAA	CCBAAADAF	DBEDFAABI	AFABEFA
1224.	LEP	Papaipema nitela*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKC	CRDBA	BDJCBDJAA	CDFCLKACM	EECDEDA
1225.	LEP	Peridroma saucia*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKC	CRDBA	BDJDBDJAA	DCFCLKADM	EECDEDA
1226.	LEP	Pseudaletia unipuncta*	CAEBABAA	NEA	CAABFA	CB	CBCM	CKC	CRBBA	BEJCBCJAA	CCFCBKACM	EEBDEDA
1227.	LEP	Spodoptera eridania*	CAEBABAA	NEA	CAABFA	DB	DBCM	CKC	CRDBA	BDJCBDJAA	CCFCLKACM	EECDEDA
1228.	LEP	Agriotis* sp.	CAEBABAA	NEA	CAABFA	DB	C CM	CKC	CRDBA	DJCBDJAA	DFCBKADM	EEADEDA
1229.	HYM	Macroxyela sp.	BACCAAAA	BDB	CAABFA	DE	DBCA	CJE	CBDBA	BCGECEBBA	CDEDDCCBA	E!CEEFA
1230.	HYM	Megaxyela* sp.	CAECABAA	DCA	CAABFA	DB	DBCM	CKC	CRDBA	BCGEBDFRA	EBFDBKADM	EEADEDA

	order	taxon	I	II	III	IV	V	VI	VII	VIII	IX	dietary data
			mouthpart	morphology	data							
1231.	HYM	*Xyela minor*	CABCAAAA	BDB	CAABFA	DB	CBBA	CJE	CFDBA	CCGGCEFKA	DCGECBBCA	E!AEEFA
1232.	HYM	*Megalodontus spissicornis**	CAECABAA	KCA	CAABFA	DB	DBCM	CKC	CRDBA	BDGEBDDGA	DCF KA M	EEBDEDA
1233.	HYM	*Neurotoma** sp.	CAECABAA	KEA	CAACFA	DB	DBCM	CKC	CDDBA	CEGEBDGKA	DCFDBKADM	EEADEDA
1234.	HYM	*Pamphilius pallipes**	CAECABAA	KCA	CAABFA	DB	DBCM	CKC	CRDBA	CDGEBCJKA	DBFDJKADM	EEADEDA
1235.	HYM	*Abia americana**	CAECABAA	MCA	CAABFA	DB	DBBM	CKC	CRDBA	BDGEBCBBA	DCFDBKADM	EEADEDA
1236.	HYM	*Cimbex americana**	CAEBABAA	MCA	CAACFA	DB	CBCM	CKC	CRDBA	BCGECCFKA	ECFDBKADM	EECDEDA
1237.	HYM	*Trichiosoma sorbi**	CAECABAA	MCA	CAABFA	CB	DBCM	CKC	CRDBA	BCGEBDJKA	FDBKADM	EE DEDA
1238.	HYM	*Hoplocampa brevis**	CAEBABAA	MCA	CAACFA	DB	DBGM	CKC	CRDBA	BDGEBDFKA	DCFDBKADM	EEADEDA
1239.	HYM	*Hoplocampa halcyon*	CACBAAAA	CDB	CAACFA	DB	DBGA	CJE	CBDBA	BCGGCBBRA	DCGEDBBCA	EGABEFA
1240.	HYM	*Macrophya pluricincta*	CACBAAAA	GDB	CAACFA	DE	CBBA	CJE	CFDBA	BDGGCEFRA	CCGEDBCBA	EG BEFA
1241.	HYM	*Pteronidea ribesii**	CAECABAA	MCA	CAABFA	DB	CBBM	CKC	CRDBA	BCGFEDFKA	DCFDBKADM	EEADEDA
1242.	HYM	*Pristiphora erichsonii*	CACBAAAA	CDB	CAABFA	DB	DBBA	CJE	CFBBA	CCGGCEFRA	DCGEDBCBA	EG BEFA
1243.	HYM	*Pristiphora erichsonii**	CAECABAA	MCA	CAACFA	DB	CBCM	CKC	CBDBA	GCGEBDFKA	ECFDBKADM	EEADEDA
1244.	HYM	*Arge macleayi**	CAECABAA	MCA	CAACFA	DB	DBCM	CKC	CRDBA	BCGCJDBBA	FCBKADM	EEADEDA
1245.	HYM	*Dolerus similis**	CAECABAA	MCA	CAACFA	DB	DBCM	CKC	CRDBA	BCGEJCFRA	DCFCJKADM	EEADEDA
1246.	HYM	*Blasticotoma filiceti**	CAECABAA	OCA	CAABFA	DB	DBBM	CKC	CRDBA	CCGEJD A	CFDJKADM	EEBDEDA
1247.	HYM	*Acordulecera** sp.	CAECABAA	MCA	CAABFA	DB	BGM	CKC	CRDBA	CDGEBDBBA	DCFDBKADM	EEADEDA
1248.	HYM	*Diprion hercyniae**	CAECABBA	MCA	CAACFA	DB	DBCM	CKC	CRDBA	BCGFBDBKA	DDFDBKADM	EEADEDA
1249.	HYM	*Xiphydria camelus**	CAECABAA	MCA	CAABFA	DB	CBBM	CKC	CRDBA	BCGDJDGKA	DCFDBKADM	RKCDEDA
1250.	HYM	*Sirex cyaneus**	CAECABAA	MDA	CAABFA	DB	DBCM	CKC	CRDBA	CDGDBDGCA	ECFEJKADM	RGBBEFA
1251.	HYM	*Tremex columba**	CAECABAA	MAA	CAABFA	DB	CBBM	CKC	CRDBA	BCGBJDBBA	DCFBJKADM	RKCDEDA
1252.	HYM	*Orussus occidentalis**	CAECAAAA	NAA	CAABFA	DB	CBBA	CAC	CBDBA	BCAAAAAAA	EBBAAAAAA	ESADFDA
1253.	HYM	*Janus compressus**	CAECABAA	OCA	CAABFA	DB	DBCM	CKC	CRDBA	CCGEBDGKA	DCFCBKADM	EJADEDA
1254.	HYM	*Apanteles flavipes**	AAECAABA	AAA	BAABCA	CE	CBBM	CKC	CBPBA	BCFBJDBAA	ECFBJKADM	ESADFDA
1255.	HYM	*Apanteles glomeratus*	CACBAAAA	CDB	CAABFA	E	CBGA	CJE	CFDBA	BCGFEBJJA	DCGDDBFBA	EGCBEFA
1256.	HYM	*Bathyaulax alami*	CACBAAAA	CDB	CAABFA	DB	CBBA	CJE	CBDBA	BCGFCEBBA	DCGDNCDBA	EGCBEFA
1257.	HYM	*Bracon gelechiae**	AAECAABA	MAA	BAABCA	DB	CBBM	CKC	CBFBA	BCJBJDBAA	ECFBJKADM	ETADFDA
1258.	HYM	*Rhogas testaceous**	AAECAABA	AAA	BAACCA	AA	CBBM	CKC	CFBBA	BCJBJDBAA	DBFBJKADM	ETADFDA
1259.	HYM	*Stenobracon dessae**	AAECAABA	MAA	BAABCA	AA	CBBM	CKC	CBFBA	BCJBJDBAA	ECFBJKADM	ETBDFDA
1260.	HYM	*Eulimneria crassifemur**	AAECAABA	AAA	BAABCA	AA	CBBM	CK	CBDBA	BCAAAAAAA	DCFBJKADM	ESADFDA
1261.	HYM	*Pimpla nucum**	AAECAABA	MAA	BAACFA	DB	DBBM	CKC	CBPBA	BCFCJDAAA	DBBAAKAAM	EQADEDA
1262.	HYM	*Xorides** sp.	AAECAABA	MAA	BAACFA	CE	DBBM	CKC	CBOBA	BCJBJDBAA	ECFBJKADM	EQADEDA
1263.	HYM	*Agriotypus armatus**	AAECABAA	MCA	CAABFA	DB	DBBM	CKC	CBDBA	CCJBJDBAA	ECFBJKADM	EQADEDA
1264.	HYM	*Apozyx penyai*	CBBCAAAA	CDB	CAABFA	CB	BBGA	CJE	CFDBA	C GFCEHJA	C GEDHJBA	E DEFC
1265.	HYM	*Pseudogonalys hahni*	CA CAAAA	BDB	CAACFA	CB	BBGA	CB	CRDBA	CCGFCEHJA	DCGDNHJBA	E DEFA
1266.	HYM	*Evania appendigaster**	AAECAABA	MAA	BAABCA	AA	CBBM	CKC	CBDBA	BBFBJDAAA	DBFBJKADM	ETBBFDA
1267.	HYM	*Gasteruption assectator**	AAECAABA	MAA	CAABFA	DB	DBCM	CKC	CBDBA	CCFBJDAAA	ECFBJKADM	EQBDEDA
1268.	HYM	*Gasteruption jaculator*	CACBAAAA	CDB	CAABFA	DB	DBEA	CJE	CDDBA	CCGGCEJCD	CDGEDFBBK	HHBCEFA
1269.	HYM	*Aulacus striatus**	AAECAABA	MAA	BAABCA	CE	CBCM	CKC	CBDBA	CCJEJDBAA	ECFCJKADM	ETABFDA
1270.	HYM	*Pelecinus* sp.	CACBAAAA	BDB	CAABFA	DB	DB A	CQE	CFDBA	BCGFCE A	DCFDD ABA	GGCBEFB
1271.	HYM	*Phaenoserphus viator**	AAEBAABA	AAA	CAABCA	CE	AAAA	CAA	COBBA	BBAAAAAAA	DBAAAAAAA	BSABFDA
1272.	HYM	*Helorus paradoxus**	CAEBAAAA	AAA	BAABCA	AA	AAAA	CAA	COBBA	AAAAAAAAA	AAAAAAAAA	PTABFDA
1273.	HYM	*Anarctopria latigaster*	CABBAAAA	IDB	CAABFA	CB	AAAA	CJA	CFBBA	CDCCB A	C FDD ABA	ESABFFA
1274.	HYM	*Platygaster herrickii**	CAEBAAAA	MAA	CAABCA	AA	AAAA	CAA	CFBBA	CBJBJDAAA	DBBBJOADA	ESABFDA
1275.	HYM	*Lygocerus testaceimanus**	AAECAABA	AAA	CAABCA	AA	DBBA	CAA	COBBA	AAAAAAAAA	EBAAAAAAA	PSABFDA
1276.	HYM	*Comedo larvarum*	CAB AAAA	IDB	CAABFA	DE	CBGA	CJE	CDFBA	BCJCICJAK	CCFBLEACN	GEABEFB
1277.	HYM	*Monodontomerus dentipes*	CABCAAAA	IDB	CAABFA	DB	CBGA	CJB	CBDBA	CCGEDBFRK	CDFDCEACN	GG BEFA
1278.	HYM	*Leucopis gigas*	CBBCAAAA	IDB	CAABFB	CE	AAAA	CJB	CBDBA	CCJEDBJAK	CCFDDGABN	H!BEEFB
1279.	HYM	*Leucopis hopei**	AAECAEBA	MAA	BAABCA	DE	DBEA	CPC	CBPBA	AAAAAAAAA	DCAAAAAAA	ETADFDA

	order	taxon	mouthpart morphology data									dietary
			I	II	III	IV	V	VI	VII	VIII	IX	data
1280.	HYM	*Axima zabriskiei**	AAECADBA	MAA	BAABCA	AA	BBBA	CAA	CFBBA	GBAAAAAAA	AAAAAAAAA	ECCDEDA
1281.	HYM	*Ceratosolen aculeatus*	CBBBAAAA	IDB	CAACFB	CE	DEMA	CJE	CDNBA	CCJCIBIAK	BBBAAEAAN	GGABEFB
1282.	HYM	*Neosycophila omeomorpha*	CACBAAAA	IDB	CAABFA	AA	AAAA	CJA	CDDBA	CCGEBCFCK	DCGDBCBCN	EFADEFC
1283.	HYM	*Blastophaga psenes.*	CABBAAAA	IAD	BAABFA	CA	AAAA	CAA	CBDBA	BBBAAAFAA	CBBAACAAA	EGABEFC
1284.	HYM	*Nasonia vitripennis**.	AAECAABA	MAA	BAABCA	DE	DBBA	CPC	CBBBA	BBFBJDAAA	DBEBJAADA	EQCDFDA
1285.	HYM	*Stenomalus liparae**	AAEBAABG	MAA	BAABCA	DE	DBBM	CKC	CFBBA	BBFBJDAAA	ECFBJKADM	ETADFDA
1286.	HYM	*Perilampus chrysopae**	AAECAABA	MAA	BAABCA	BE	AAAA	CPA	COBBA	BBAAAAAAA	DBAAAAAAA	ETABFDA
1287.	HYM	*Perilampella raphidophorae.*	CABCAAAA	IDB	CAABFA	CE	AAAA	CJA	CDDBA	CDGCBBBA	C FDD ABA	E EFB
1288.	HYM	*Schizaspidia tenuicornis**	AAEAAABA	MAA	ABBCCB	AA	CEEA	CGC	AAAAA	BBAAAAAAA	DBAAAAAAA	PTABFDA
1289.	HYM	*Arachnophaga picea**	CAECAABA	MAA	CAABCA	CB	AAAA	CAA	COBBA	AAAAAAAAA	DBAAAAAAA	BSABFDA
1290.	HYM	*Isodromus iceryae**.	AAEBAABA	AAA	CAABCA	AA	AAAA	CAA	COBBA	AAAAAAAAA	AAAAAAAAA	PTABFDA
1291.	HYM	*Myiocnema comperei.*	CABBAAAA	IDB	CAABCA	CB	CBIA	CJE	CBDBA	BBJDCBPAA	CBECDAACA	ERABFFB
1292.	HYM	*Pnigalio mediterraneus**	AAEBAABA	MAA	CAABCA	CB	AAAA	CAA	COBBA	AAAAAAAAA	DBAAAAAAA	PFABEDA
1293.	HYM	*Tetrastichus chrysopae**	AAEBAABA	AAA	CAABCA	AA	AAAA	CAA	COBBA	AAAAAAAAA	AAAAAAAAA	BTABFDA
1294.	HYM	*Apseudogramma popei*	CABBAAAA	IDB	CAABCA	CB	CBIA	CJE	CRDBA	BBJCFCPAA	CBECBAACA	ERABFFB
1295.	HYM	*Anagrus incarnatus**	CAEBAAAA	AAA	BAABCA	AA	AAAA	CAA	COBBA	AAAAAAAAA	AAEBCAADA	BSCBFDA
1296.	HYM	*Ibalia leucospoides**.	AAECAABA	MAA	CAABCA	DB	DBCM	CKC	CBDBA	BCAAAAAAA	DBBAAKAAM	ESADFDA
1297.	HYM	*Figites anthomyiarum**	CAEBAAAA	MAA	AAABCA	AA	AAAA	DAA	AAAAA	AAFBJDAAA	AAEBJAADA	GSABFDA
1298.	HYM	*Rhodites rosae**	AAECAABA	MAA	CAABFA	DB	DBGM	CKC	CRDBA	BBJBJDAAA	ECBAAKAAM	EEADEDA
1299.	HYM	*Plumarius* sp.	CABBAAAA	FAD	BAABCA	CB	DBGA	CJC	CFDBA	CCFFCBAAK	DBEDDAABN	E BFB
1300.	HYM	*Chrysis shanghaiensis**.	AAECAABA	AAA	BAABCA	DB	DBIM	CKE	CBDBA	BBJBJDBAA	DBFBJKADM	PTADFDA
1301.	HYM	*Tetrodontochelys ljunghii*	CABCAAAB	IDB	CAABFA	DB	CB A	CJ	CFDBA	BCGCCCFRA	CBFCDEACA	GQADEFB
1302.	HYM	*Scolebythus madecassus.*	CABCAAAA	IDD	CAABCA	DB	AAAA	CJA	CCDBA	BCFGCCAAA	CBEEDAACA	FB
1303.	HYM	*Parasierola gallicola**.	AAEBAABA	MAA	CAABCA	AA	AAAA	CAA	COBBA	CBJBJDBAA	DBFBJBADA	PTADFDA
1304.	HYM	*Pristocera armifera*	CABCAAAA	IDD	BAABFA	DB	AAAA	CJA	CFDBA	BCJGCBFBK	DCFDDFABN	EQABEFC
1305.	HYM	*Elaphroptera erythrura**	AAEBAABA	MCA	BAABCA	DB	CBCM	CKC	CBDBA	BCJBJDBAA	DCFCJKADM	PTADFDA
1306.	HYM	*Fedtschenkia grossa*	CCC BAAA	NDB	CDABCB	CE	B J	CJK	CFDBA	CDJGEBKAJ	BDFENGABK	IGCBEFB
1307.	HYM	*Mutilla lunulata**	AAECAABA	MAA	CAABCA	DB	DBCM	CKC	CFDBA	BCJBJDBAA	DBFBJKADM	PTADFDA
1308.	HYM	*Bradynobaenus* sp.	CBCBAAAA	IDD	BAABCA	CB	DBBA	CJM	CBDBA	CCFCJDAAK	DCGDDCCCN	E FB
1309.	HYM	*Rhopalosoma** sp.	AAECAABA	MCA	CAABCA	DE	DBCM	CKC	CBIBA	CCGBJDGRA	DBGBJKEDM	PTABFDA
1310.	HYM	*Dipogon sayi**	AAECAAAA	MAA	CAABCA	DE	DBFM	CKC	CBDBA	BCGBJDGLA	EBFBJKADM	EQBDGDA
1311.	HYM	*Pepsis thisbe**.	AAECAABA	MAA	CAABCA	AA	DBBM	CKC	CRDBA	BBGBJDGLA	EBFBJKADM	EQBDGDA
1312.	HYM	*Pseudagenica carbonaria**.	AAECAABA	MAA	CAABCA	DE	DBCM	CKC	CBDBA	BCGBJDGBA	EBFBJKADM	ETABFDA
1313.	HYM	*Aphaenogaster subterranea**.	AAECAABA	MAA	BAABCA	CB	CBBA	CQC	CBDBA	BCGBJDGBA	DBFBJBADA	EQCDGDA
1314.	HYM	*Atta sexdens.*	CACBAAAA	IAD	BAABCA	CB	DBBA	CJC	CFDBA	CCGECBIJK	CDGCDEEFN	GOADGFD
1315.	HYM	*Camponotus ligniperda*	CABBAAAA	IAD	BAABCA	DB	DBCA	CJN	CFDBA	CDGGCEIJK	CDGEDEDFN	G&CDGFD
1316.	HYM	*Camponotus vagus**	AAECAABA	MAA	BAABCA	CE	CBGA	CQC	CBDBA	BCGBJDGRA	DBFBJBADA	E@ABGDA
1317.	HYM	*Cataglyphis bicolor*	CABBAAAA	IDD	BAABCA	DB	CBGA	CJN	CFDBA	CDGGCEIJK	CDGEDEDFN	GQCDGFD
1318.	HYM	*Dolichoderis garbei*	CABBAAAA	IAD	BAABCA	DB	B A	CJN	CFDBA	CDGGCEIJK	CDGEDEDFN	GGABGFD
1319.	HYM	*Dorylus wilverthi*	CAEBAAAA	IAA	BAABCA	CB	D GA	J	CFDBA	BCGCJDIMK	CDGCDEDFN	GQCDGFD
1320.	HYM	*Ection burchelli.*	CCBBAAAA	IAB	BAABCA	CB	DBGA	CJN	CGDBA	CCGCCBIJK	DCGD BDBN	EQCDGFD
1321.	HYM	*Formica rufa**	AAECAABA	MAA	CAABCA	AA	CBCM	CKC	CBDBA	BCGBJDGLA	DBSBJKFDM	P@ABGDA
1322.	HYM	*Messor structor*	CACBAAAA	IAD	BAABCA	DB	DBCA	CJN	CFDBA	CDGECEIJK	CDGDDEDFN	GCCDGFB
1323.	HYM	*Oecophylla smarogdina*	CACBAAAA	IAD	BAABCA	CB	DBGA	CJN	CFFBA	CDGFEEIJK	CCGENEDBN	GOCDEFD
1324.	HYM	*Paltothyreus tarsatus*	CACBAAAA	IAD	BAABCA	BB	CBCA	CJN	CFDBA	CCGECBIJK	DDGEDEDFN	GQBDGFD
1325.	HYM	*Scolia bidens*	CCCCBAAA	FDB	CDABBB	CB	DBBJ	BJK	CFFBA	CEJGCBKAJ	BDGENGGCK	IGCBEFB
1326.	HYM	*Paragia odyneroides*	CDCCCAAA	IDB	CDABBB	CB	BBBJ	BJB	CNDBA	BCGGEEKJJ	DCGENGGBK	IG BEFB
1327.	HYM	*Eumenes unguiculus**	AAECAABA	MAA	CAABCA	DB	DBBA	CQC	CBDBA	CCGBJDGBA	DBFBJBADA	ETABFDA
1328.	HYM	*Polistes galliacus**	AAECABBA	MAA	CAABCA	DE	DBBM	CKC	EFDBA	BCJBJDGAA	DBFBJKADM	EQCBEDA

	order	taxon	mouthpart morphology data									dietary
			I	II	III	IV	V	VI	VII	VIII	IX	data
1329.	HYM	*Polistes olivaceous*	CACBAAAA	IDB	CAABCA	CB	DBDA	CFE	CDDBA	CCGGCEIJK	CCGEDEEBN	GGCBEFA
1330.	HYM	*Vespa vulgaris*	EBCBAAAA	IDB	CDABBB	CB	BBNJ	BJK	CBDBA	CCGGEEIRJ	CCGEDGEFK	I&CEEFA
1331.	HYM	*Vespula germanica*	CBCCAAAA	IDB	CDABBB	CB	CBGJ	BJK	CDHBA	CCGGCEHJJ	CCGEDGCFK	I@CEEDA
1332.	HYM	*Vespula sylvestris**	CAECABBA	MAA	CAABCA	CB	DBCM	CKE	CRDBA	BCGBJDGBA	DBFBJKADM	E@CEEDA
1333.	HYM	*Ammophila campestris**	CAECAABA	MAA	CAABCA	DB	DBCM	CKC	CFDBA	BCGBJDGBA	BCFBJKADM	E@BDDDA
1334.	HYM	*Ammophila sabulosa*	CCCBBAAA	IDB	CDABBB	CB	BB J	BJK	CFDBA	BCGGCEKIJ	BCGEDGGFK	E&CEEFA
1335.	HYM	*Chalybion bengalense*	CBCBBAAA	IDB	CAABCB	CB	DBGA	CJC	CFLBA	CCGGEEIJK	CDGENEJBN	GGCBEFA
1336.	HYM	*Prionyx thomae*	CCABAAAA	IDB	CDABBB	CB	CBEJ	BJK	CFDBA	CCGGCEKJJ	CDGBDG CK	I&CEEFA
1337.	HYM	*Sphex ichneumoneus*	CCABAAAA	IDB	CDABBB	DB	CBEJ	BJK	CFCBA	CCGGEEKJJ	CDGENG FK	I!BEEFA
1338.	HYM	*Tachytes distinctus*	CBABAAAA	IDB	CDABBB	DB	DBEJ	BJB	CFDBA	CCGGCEKJJ	CDGEDGCFK	IGCBEFA
1339.	HYM	*Colletes fulgidus*	CCACBAAA	IDB	CDABBB	CB	DBBJ	BJB	CFDBA	CCGGEBKJJ	CDGEDGEBK	I!CEEFC
1340.	HYM	*Diphaglossa gayi*	CCCBBAAA	CDB	CDABBB	CB	DB J	BJB	CFDBA	CCGGIEKCJ	CDGEDGEFK	IGCBEFA
1341.	HYM	*Hylaeus* sp.	CBCCBAAA	IDB	CDABBB	CB	DBGJ	BJB	CFDBA	CCGGCEKBJ	CDGEDGEBK	I!CEEFA
1342.	HYM	*Halictus farinosus*	CCABBAAA	IDB	CDABBB	CB	DBGJ	BJB	CFDBA	CCGGCEKJJ	CDGENGKFK	IHCCEFA
1343.	HYM	*Nomia melanderi*	CDCCBAAA	IDB	CDABBB	CB	CBNJ	BJB	CFDBA	CCJGCBKAJ	BDGEDGGBK	IGCBEFA
1344.	HYM	*Sphecodes* sp.	CCACBAAA	IDB	CDABBB	CB	DB J	BJB	CFDBA	CCJGCEKAJ	CCGEDGKBK	I!CDEFA
1345.	HYM	*Andrena mimetica*	CCCCBAAA	IDB	CDABBB	CB	DBGJ	BJB	CFDBA	CCGGCEKJJ	BCGENGKBK	IGBBEFA
1346.	HYM	*Andrena** sp.	CAECAABA	MAA	BAABCA	DB	DBIM	CK	CFDBA	BCKBJDABA	DBFBJKADM	E!CEGDA
1347.	HYM	*Panurgus* sp.	CCCCBAAA	IDB	CDABBB		DBGJ	BJB	CFDBA	CCGGCEKBJ	BCGEDGGBK	I!BDEFA
1348.	HYM	*Protoxaea gloriosa**	CAEBAABA	MAA	BAABCA	CB	CBJA	CKE	CFIBA	EBFBJDAAA	CBFBJKADM	E!CEDDA
1349.	HYM	*Macropis* sp.	CCACBAAA	IDB	CDABBB		DB J	BJB	CF BA	CCGGCEKCJ	BCGEDGKFK	IG BEFA
1350.	HYM	*Anthidium atripes*	CDACBAAA	IDB	CDABBB	CB	CBBJ	BJB	CFDBA	CCGFIEKCJ	BCGEHGEFK	IGCBEFA
1351.	HYM	*Fidelia villosa**	CAECAABA	MAA	BAABCA	DB	DBEM	CKE	CBDBA	CBKBJDABA	DBFBJKADM	EHACDDA
1352.	HYM	*Megachile* sp.	CDABBAAA	IDB	CDABBB	CB	CBBJ	BJB	CBDBA	CCGCIDKCJ	BCGEHGEFK	IGBBEFA
1353.	HYM	*Osmia* sp.	CDABBAAA	IDB	CDABBB	DB	DBGJ	BJB	CFDBA	CCGDICKCJ	BDGEHGEFK	IGCBEFA
1354.	HYM	*Anthophora edwardsi*	CDCBBAAA	IDB	CDABBB	CB	CBBM	BJB	CNABA	CCGGIBKCJ	BDGEHGEFK	IGCBEFA
1355.	HYM	*Anthophora stanfordiana**	CAECAABA	MAA	CAABCA	DB	DBBM	CKE	CBBBA	BCGBJDGBA	DBFBJKADM	E!CEGDA
1356.	HYM	*Eucera* sp.	CDCBBAAA	IDB	CDABBB	DB	CBBJ	BJB	C BA	CCGFIBKRJ	BDGEHGGFK	IGCBEFA
1357.	HYM	*Triepeolus remigatus**	CAEBAAAA	MAA	BAABCA	AA	BBIA	CAA	CFABA	DBAAAAAAA	CCEBLAABA	E@ADFDA
1358.	HYM	*Xylocopa virginica**	CAECAABA	MAA	BAABCA	DB	DBMM	CKE	CBDBA	CCKBJDABA	DBFBJKADM	E!CBEDA
1359.	HYM	*Apis mellifera*	CDCBBAAA	IDB	CDABBB	CB	DBSJ	BJB	CNABA	CCGBICKJJ	BDGEHGCFK	IGCBEFA
1360.	HYM	*Apis mellifera**	CAECABBA	MAA	BAABCA	CB	DBBM	CKE	CBBBA	BCKBJDABA	DBFBJKADM	E@ABEDA
1361.	HYM	*Bombus americanorum**	CAECAABA	MAA	BAABCA	DD	DECM	CKE	CBBBA	CBKBJDABA	DBFBJKADM	E@ABEDA
1362.	HYM	*Bombus vosnesenskii*	CDCBBAAA	IDB	CDABBB	CB	DBGJ	BJB	CNABA	CCGCICKJJ	BDGEHGCFK	IGCBEFA
1363.	HYM	*Psithyrus* sp.	CDABBAAA	IDB	CDABBB	CB	DBGJ	BJB	CNABA	CCGCICKJJ	BDGEHGKFK	IG BEFA
1364.	HYM	*Trigona cupira**	CAECAABA	MAA	BAABCA	DB	DBBM	CKE	CFDBA	CBKBJDABA	EBFBJKADM	E@ABEDA
1365.	HYM	*Trigona scaptotrigona*	CDCCBAAA	IDB	CDABBB	CB	DBGJ	BJB	CNLBA	CCGCICK J	BDGEHG BK	I!CDDFB

APPENDIX D
EXTANT HEXAPOD DIVERSITY
(Families in Orders, Genera in Families, and Species in Genera)*

PROTURA		
Acerentomidae	13	136
Proentomidae	7	28
Sinentomidae	1	1
Eosentomidae	1	105
(4 families)	22	270
COLLEMBOLA		
So. **Arthropleona**		
Sf. **Hypogastruoidea**		
Onychiuridae	26	300
Hypogastruridae	29	400
Sf. **Entomobryoidea**		
Entomobryidae	85	1200
Isotomidae	76	700
Oncopoduridae	3	20
Tomoceridae	12	80
So. **Neoarthropleona**		
Brachystomellidae	22	80
Anuridae	24	170
Setanuridae	5	6
Neanuridae	42	250
Uchidanuridae	3	3
So. **Metaxypleona**		
Poduridae	1	5
Actaletidae	2	2
So. **Sympleona**		
Neelidae	3	25
Smithuridae	46	550
(15 families)	388	3800
DIPLURA		
So. **Rhabdura**		
Sf. **Projapygoidea**		
Anajapygidae	1	7
Projapygidae	1	18
Sf. **Campodeoidea**		
Procampodeidae	1	1
Campodeidae	31	419
So. **Dicellurata**		
Japygidae	30	263
Parajapygidae	1	40
(6 families)	65	748
ARCHAEOGNATHA		
Machilidae	35	280
Meinertellidae	15	134
(2 families)	50	414
THYSANURA		
Lepidotrichidae	1	1
Lepidmatidae	20	80
Maindroniidae	1	3
Nicoletiidae	50	150
(4 families)	72	320
EPHEMEROPTERA		
So. **Schistonota**		
Sf. **Baetoidea**		
Siphlonuridae	22	123
Ametropodidae	1	5
Baetidae	20	520
Metretopodidae	2	8
Oligoneuriidae	1	3
Heptageniidae	30	380
Sf. **Leptophlebiioidea**		
Leptophlebiidae	68	380
Sf. **Ephemeroidea**		
Behningiidae	3	5
Potamanthidae	7	27
Euthyplociidae	7	12
Polymitarcyidae	6	70
Ephemeridae	8	99
Palengeniidae	6	31
So. **Pannota**		
Sf. **Ephemerelloidea**		
Ephemerellidae	7	163
Tricorythidae	13	122
Sf. **Caenoidea**		
Neoephemeridae	3	10
Caenidae	9	85
Baetiscidae	1	12
Sf. **Prosopistomatoidea**		
Prosopistomatidae	1	11
(19 families)	227	2200
ODONATA		
So. **Zygoptera**		
Sf. **Lestinoidea**		
Perilestidae	6	30
Chlorolestidae	8	31
Lestidae	8	150
Sf. **Hemiphleboidea**		
Hemiphlebiidae	1	1
Sf. **Coenagrionoidea**		
Platystictidae	4	135
Megapodagrionidae	37	210
Protoneuridae	20	230
Platycnemidae	23	160
Lestoideidae	1	2
Coenagrionidae	72	1100
Pseudostigmatidae	5	20
Sf. **Calopterygoidea**		
Amphipterygidae	4	12
Chlorocyphidae	17	125
Heliocharitidae	4	11
Polythoridae	9	60
Epallagridae	11	60
Calopterygidae	16	175
So. **Anisozygoptera**		
Epiophlebiidae	1	2
So. **Anisoptera**		
Sf. **Aeshnoidea**		
Gomphidae	84	810
Petaluridae	5	9
Aeshnidae	47	390
Sf. **Cordulegasteroidea**		
Cordulegasteridae	6	60
Sf. **Libelluloidea**		
Synthemidae	4	32
Corduliidae	43	340
Libellulidae	143	950
(25 families)	579	5100
BLATTODEA		
Cryptocercidae	1	8
Blattidae	44	525
Polyphagidae	39	192
Blatellidae	209	1740
Blaberidae	155	1020
(5 families	1448	3500
MANTODEA		
Chaeteessidae	1	
Metallyticidae	1	
Mantoididae	1	
Eremiaphilidae	2	
Amorphoscelidae	11	
Hymenopodidae	43	
Empusidae	8	
Mantidae	263	
(8 families)	330	1800
ISOPTERA		
Mastotermitidae	1	1
Kalotermitidae	21	293
Hodotermitidae	8	30
Rhinotermitidae	13	159
Serritermitidae	1	1
Termitidae	181	1505
(6 families)	225	2000

GRYLLOBLATTODEA		
Grylloblattidae	3	13
(1 family)		
ORTHOPTERA		
So. Ensifera		
Sf. Stenopelmatoidea		
Lexinidae	1	10
Stenopelmatidae	6	33
Cooloolidae	1	2
Gryllacrididae	76	550
Mimnermidae	40	150
Sf. Raphidophoroidea		
Macropathidae		
Raphidophoridae	30	250
Sf. Hagloidea		
Prophlangopsidae	2	4
Sf. Tettigonoidea		
Bradyporidae	28	200
Acridoxenidae	1	2
Phaneropteridae	300	2000
Pseudophyllidae	250	1000
Meconematidae	29	200
Phasmodidae	4	4
Phylloporidae	10	60
Mecopodidae	57	130
Tettigoniidae	80	375
Conocephalidae	140	1000
Sf. Schizodactyloidea		
Schizodactylidae	3	7
Sf. Gryllotalpoidea		
Gryllotalpidae	6	65
Sf. Grylloidea		
Gryllidae	100	800
Pentacentridae	15	50
Trigonidiidae	25	275
Phalangopsidae	60	230
Eneopteridae	78	500
Scleropteridae	3	16
Pteroplistidae	1	5
Cachoplistidae	1	3
Mogoplistidae	14	184
Myrmecophilidae	5	45
Oecanthidae	3	67
So. Caelifera		
Sf. Eumastacoidea		
Chlorotypidae	18	70
Eruciidae	22	60
Mastacideidae	2	8
Euschmidtiidae	60	236
Thericleidae	56	206
Miraculidae	6	21
Episactidae	6	22
Eumastacidae	18	100
Gomphomastacidae	8	27
Biroellidae	1	26
Morabidae	41	243
Sf. Prosopoidea		
Prosopiidae	17	130
Sf. Trigonopterygoidea		
Boreacrididae	2	2
Trigonopterygidae	3	13
Sf. Xyronotoidea		
Xyronotidae	1	2
Tanaoceridae	2	3
Sf. Pneumoroidea		
Pneumoridae	9	17
Sf. Acridoidea		
Pamphagodidae	4	5
Pamphagidae	80	320
Tristiridae	19	27
Lathiceridae	4	5
Pyrgomorphidae	144	452
Lentulidae	20	60+
Ommexechidae	12	31
Romaleidae	80	200+
Pauliniidae	2	4
Acrididae	1100	7000+
Sf. Tetrigoidea		
Tetrigidae	170	850
Batrachideidae	16	90
Sf. Tridactyloidea		
Ripipterygidae	2	62
Tridactylidae	7	80+
Sf. Cylindroachetoidea		
Cylindrachetidae	2	7
(63 families)	3300	18,700
PHASMATODEA		
So. Tinematodea		
Sf. Tinematoidea		
Tinematidae	1	9
So. Phasmatoidea		
Sf. Bacilloidea		
Bacillidae	52	300+
Bacunculidae	52	300
Sf. Phylloidea		
Phyllidae	3	20
Sf. Necroscerioidea		
Necrosciidae	70+	500
Heteronemiidae	19	100+
Lonchodidae	25	200
Pachymorphidae	24	200+
Palophidae	4	10
Sf. Phasmatoidea		
Bacteriidae	17	124
Phasmatidae	87	500
(11 families)	354	2300
DERMAPTERA		
So. Forficulina		
Sf. Pygidicranoidea		
Pygidicranidae	16	130
Karschiellidae	2	12
Diplatyidae	4	140
Sf. Labiduroidea		
Carcinophoridae	35	300
Labiduridae	7	60
Apachyidae	2	16
Sf. Forficuloidea		
Labiidae	35	380
Chelisochidae	15	72
Forficulidae	68	380
So. Hemimerina		
Hemimeridae	2	11
So. Arixeniina		
Arixeniidae	2	5
(11 families)	188	1500
EMBIOPTERA		
Clothidae	2	12
Embiidae	75	250
Notoligotomidae	4	24
Embonychidae	1	1
Anisembiidae	13	[300]
Australembiidae	2	2
Oligotomidae	6	[200]
Teratembiidae	13	[1200]
(8 families)	116	2000
PLECOPTERA		
So. Arctoperlaria		
Sf. Nemouroidea		
Nemouridae	17	400
Notonemouridae	16	60
Capniidae	16	250
Leuctridae	12	200
Taeniopterygidae	13	100
Scopuridae	1	2
Sf. Subulipalpia		
Perlidae	48	375
Perlodidae	40	250
Chloroperlidae	18	125
Peltoperlidae	13	35
Pteronarcyidae	3	13
So. Anarctoperlaria		
Sf. Eusthenoidea		
Diamphipnoidae	2	5
Eustheniidae	6	17
Sf. Leptoperloidea		
Austroperlidae	9	12
Gripopterygidae	37	120
(15 families)	251	2000

ZORAPTERA		
Zorotypidae	1	24
(1 family)		
PSOCOPTERA		
So. Trogiomorpha		
Sf. Atropetae		
Lepidopsocidae	15	144
Trogiidae	5	24
Psoquillidae	4	22
Sf. Psocatropetae		
Psyllipsocidae	4	26
Prionoglaridae	1	2
So. Troctomorpha		
Sf. Nanopsocetae		
Liposcelidae	8	144
Pachytroctidae	6	51
Sphaeropsocidae	2	12
Sf. Amphientometae		
Amphientomidae	13	62
Musapsocidae	1	5
Troctopsocidae	4	11
Manicapsocidae	3	5
Compsocidae	2	2
So. Psocomorpha		
Sf. Epipsocetae		
Epipsocidae	6	89
Dubellapsocidae	3	17
Spurostigmatidae	2	11
Philoneuridae	4	21
Sf. Caecilietae		
Asiopsocidae	1	2
Caeciliidae	17	355
Amphipsocidae	10	90
Stenopsocidae	4	43
Polypsocidae	2	18
Sf. Homilopsocoidea		
Elipsocidae	21	74
Philotarsidae	7	143
Mesopsocidae	5	34
Lachesillidae	4	107
Peripsocidae	2	113
Ectopsocidae	3	124
Hemipsocidae	2	14
Calopsocidae	4	9
Pseudocaeciliidae	15	117
Trichopsocidae	1	5
Archipsocidae	3	53
Sf. Psocetae		
Psocidae	31	494
Thrysophoridae	2	22
Psilopsocidae	1	6
Myopsocidae	4	109
(37 families)	222	2600
ANOPLURA		
Echinophthiriidae	5	12
Enderleinellidae	5	49
Haematopinidae	1	22
Hamophthiriidae	1	1
Hoplopleuridae	5	132
Hybophthiridae	1	1
Linognathidae	3	70
Microthoraciidae	1	4
Neolinognathidae	1	2
Pecaroecidae	1	1
Pedicinidae	1	16
Pediculidae	1	2
Polyplacidae	14	175
Pthiridae	1	2
Ratemiidae	1	2
(15 families)	42	491
MALLOPHAGA		
So. Amblycera		
Menoponidae	69	750
Laemobothridae	1	40
Ricinidae	3	50
Boopidae	9	25
Trimenoponidae	7	20
Abrocomophagidae	1	1
Gyropidae	8	80
So. Ishnocera		
Trichodectidae	20	300
Philopteridae	122	1500
Heptapsogasteridae	18	200
So. Rhynchopthirina		
Haematomyzidae	1	2
(11 families)	259	3000
THYSANOPTERA		
So. Terebrantia		
Aeolothripidae	30	230
Heterothripidae	12+	90+
Merothripidae	4	20
Thripidae	200	1500
So. Tubulifera		
Phlaeothripidae	300	[7000]
(5 families)	550	8800
HETEROPTERA		
So. Enicocephalomorpha		
Sf. Enicocephaloidea		
Enicocephalidae	38	130
So. Dipscomorpha		
Sf. Dipscoroidea		
Dipscocoridae	2	20
Ceratocombidae	6	30
Hypsipterygidae	1	3
Schizopteridae	33	155
So. Nepomorpha		
Sf. Nepoidea		
Nepidae	12	200
Belostomatidae	8	100
Sf. Corixoidea		
Corixidae	40	300
Sf. Gelastocoroidea		
Gelastocoridae	2	150
Ochteridae	3	32
Sf. Naucoroidea		
Naucoridae	36	150
Aphelocheiridae	1	20
Sf. Notonectoidea		
Notonectidae	9	200+
Pleidae	3	20+
Helotrephidae	12	15+
So. Gerromorpha		
Mesoveliidae	7	30+
Hydrometridae	7	100
Hebridae	6	120
Paraphrynoveliidae	1	2
Macroveliidae	3	3
Veliidae	29	420
Madeoveliidae	1	1
Gerridae	56	450+
Hermatobatidae	2	10
So. Leptopodomorpha		
Omaniidae	2	4
Saldidae	19	230
Leotichiidae	1	2
Leptopodidae	5	24
So. Cimicomorpha		
Thaumastocoridae	6	15
Joppeicidae	1	1
Sf. Tingoidea		
Tingidae	235	1800
Vianaididae	5	5
Sf. Miroidea		
Miridae	1000	10,000
Microphysidae	7	25
Sf. Cimicoidea		
Velocipedidae	2	4
Medocostidae	1	2
Nabidae	40	300
Plokiophilidae	4	13
Anthocoridae	80	500
Cimicidae	23	75+
Polyctenidae	5	31
Sf. Reduvoidea		
Pachynomidae	4	15
Reduviidae	1000	5000+

So. **Pentatomorpha**		
Sf. **Aradoidea**		
Aradidae	150+	1000+
Termitaphididae	2	9
Idiostolidae	3	4
Piesmatidae	4	20
Colobathristidae	22	90
Berytidae	35	100+
Malcidae	3	20+
Lygaeidae	476	3000+
Pyrrhocoridae	38	300+
Largidae	15	100
Sf. **Coreoidea**		
Stenocephalidae	2	33
Hyocephalidae	1	1+
Coreidae	250	1800
Alydidae	42	250
Rhopalidae	18	142
Sf. **Pentatomoidea**		
Thaumastellidae	1	2
Urostylidae	6	90
Plataspidae	40	500
Aphylidae	1	2
Lestoniidae	1	3
Cydnidae	71	300+
Thyreocoridae	9	100+
Megarididae	1	16
Conopidae	1	8
Scutelleridae	100	400
Dinidoridae	12	100+
Tessaratomidae	37	243
Eumenotidae	1	3
Pentatomidae	400	5000
Acanthosomatidae	12	180+
Phloeidae	2	3
(74 families)	4500	34,500
HOMOPTERA		
So. **Coelorrhyncha**		
Peloridiidae	10	20
So. **Auchenorrhyncha**		
Sf. **Fulgoroidea**		
Cixiidae	120	1000
Tettigometridae	12	70
Delphacidae	150	1300
Eubrachyidae	31	180
Fulgoridae	120	700
Achilidae	100	350
Tropiduchidae	110	300
Issidae	210	1000+
Lophopidae	41	120
Acanaloniidae	13	81
Ricaniidae	41	120
Flatidae	212	1000
Derbidae	120	800
Achilixiidae	3	9
Meenoplidae	11	80
Kinnaridae	8	42
Dictyopharidae	130	540
Gengidae	2	2
Nogodinidae	41	140
Hypochthonellidae	1	1
Sf. **Cercopoidea**		
Cercopidae	330	2300
Sf. **Cicadoidea**		
Cicadidae	140	1500
Sf. **Cicadelloidea**		
Cicadellidae	1500	20,000
Sf. **Membracoidea**		
Membracidae	320	2400
Aetalionidae	8	50
Biturritiidae	4	10
Nicomiidae	5	15
So. **Sternorrhyncha**		
Sf. **Psylloidea**		
Psyllidae	150	1300
Sf. **Aleyrodoidea**		
Aleyrodidae	126	1156
Sf. **Aphidoidea**		
Aphididae	350	3500
Adelgidae	8	50
Phylloxeridae	12	60
Sf. **Coccoidea**		
If. **Archaeococcoidea**		
Ortheziidae	6	81
Margarodidae	50	250
Phenacoleachiidae	2	2
If. **Neococcoidea**		
Stictococcidae	3	15
Putoidae	3	48
Pseudococcidae	180	1100
Coccidae	90	1000
Aclerdidae	3	50
Dactylcppidae	1	9
Kermesidae	4	68
Cryptococcidae	2	5
Eriococcidae	50	350
Apiomorphidae	3	62
Kerridae	7	65
Beesoniidae	2	3
Lecanodiaspididae	9	71
Cerococcidae	3	64
Asterolecaniidae	23	200
Conchaspididae	2	23
Phoenicococcidae	2	2
Halimococcidae	4	17
Diaspididae	350	1500
(55 families)	5200	45,400
MEGALOPTERA		
Corydalidae	16	200
Sialidae	4	60
(2 families)	20	260
RAPHIDOIDEA		
Raphidiidae	3	75
Inocellidae	2	25
(2 families)	5	100
PLANIPENNIA		
Sf. **Ithonoidea**		
Ithonidae	6	22
Polystoechotidae	3	3
Sf. **Coniopterygoidea**		
Coniopterygidae	19	250+
Sf. **Mantispoidea**		
Dilaridae	[10]	48
Berothidae	23	57
Mantispidae	15+	250
Sf. **Osmyloidea**		
Neurorthidae	3	9
Osmylidae	25	100+
Sisyridae	3	48
Sf. **Hemerobioidea**		
Hemerobiidae	80	800+
Chrysopidae	90	1500+
Sf. **Myrmeleontoidea**		
Psychopsidae	3	6
Nemopteridae	40	130
Nymphidae	6	15
Ascalaphidae	65	400
Stilbopterygidae	3	9
Myrmeleontidae	300+	600+
(17 families)	700	4200
COLEOPTERA		
So. **Archostemmata**		
Ommatidae	3	5
Cupedidae	4	21
Micromalthidae	1	1
So. **Myxophaga**		
Lepiceridae	1	2
Torridincolidae	6	25
Sphaeriidae	1	18
Hydroscaphidae	3	13
So. **Adephaga**		
Rhysodidae	18	150
Carabidae	1500	30,000
Haliplidae	4	200

Amphizoidae	1	5
Hygrobiidae	1	4
Noteridae	12	175
Dytiscidae	120	3000
Gyrinidae	11	700
So. Polyphaga		
Sf. Staphylinoidea		
Hydraenidae	15	400
Ptiidae	67	430
Agyrtidae	8	60
Leiodidae	250	2000
Leptinidae	3	6
Platypsyllidae	1	1
Scydmaenidae	75	2000
Micropeplidae	3	43
Dasyceridae	1	11
Silphidae	14	175
Staphylinidae	1500	30,000
Pselaphidae	650	5000
Sf. Hydrophiloidea		
Hydrophilidae	125	2000
Georyssidae	1	25
Sphaeritidae	1	3
Synteliidae	1	4
Histeridae	200	3000
Sf. Eucinetoidea		
Eucinetidae	5	30
Clambidae	5	50
Scirtidae	30	600
Sf. Dascilloidea		
Dascillidae	15	80
Rhipiceridae	5	50
Sf. Scarabaeoidea		
Lucanidae	100	1200
Passalidae	27	500
Trogidae	5	300
Ceratocanthidae	20	200
Pleocomidae	1	35
Geotrupidae	45	600
Diphyllostomatidae	1	3
Scarabaeidae	2000	25,000
Sf. Byrrhoidea		
Byrrhidae	28	300
Sf. Buprestoidea		
Buprestidae	400	15,000
Sf. Dryopoidea		
Eulichadidae	2	12
Callirhiphidae	8	150
Ptilodactylidae	35	300
Chelonariidae	2	300
Heteroceridae	15	300
Limnichidae	30	200
Lutrochidae	1	15
Dryopidae	12	200
Elmithidae	90	700
Psephenidae	20	100
Sf. Elateroidea		
Artematopidae	8	60
Cerophytidae	1	7
Elateridae	400	9000
Cebrionidae	11	170
Throscidae	4	190
Perothopidae	1	3
Eucnemidae	190	1200
Rhinorhipidae	1	1
Sf. Cantharoidea		
Brachypsectridae	1	3
Cneoglossidae	1	7
Homalisidae	1	10
Lycidae	150	3500
Drilidae	6	80
Phenogodidae	35	200
Telegeusidae	2	6
Lampyridae	100	2000
Omethidae	6	10
Cantharidae	135	5000
Sf. Dermestoidea		
Derodontidae	4	19
Nosodendridae	1	50
Dermestidae	45	850
Jacobsoniidae	6	7
Sf. Bostrichoidea		
Bostrichidae	90	700
Anobiidae	140	1600
Ptinidae	40	450
Sf. Lymexyloidea		
Lymexylidae	6	50
Sf. Cleroidea		
Phoiophilidae	1	1
Trogossitidae	60	600
Chaetosomatidae	2	2
Cleridae	150	4000
Phycosecidae	1	4
Acanthocnemidae	1	1
Melyridae	200	5000
Sf. Cucujoidea		
Protocucujidae	1	3
Sphindidae	6	35
Nitulidae	160	3000
Rhizophagidae	20	250
Boganiidae	4	4
Phloeostichidae	6	8
Helotidae	1	100
Cucujidae	75	1200
Cavognathidae	4	4
Cryptophagidae	30	600
Propalticidae	2	35
Lamingtoniidae	1	1
Hobartiidae	1	1
Languriidae	80	900
Erotylidae	30	2500
Phalacridae	55	600
Cerylonidae	55	650
Corylophidae	35	400
Discolomidae	18	400
Coccinellidae	500	4500
Sphaerosomatidae	1	50
Endomychidae	120	1300
Lathridiidae	25	500
Biphyllidae	6	200
Bituridae	7	25
Sf. Tenebrionoidea		
Mycetophagidae	18	200
Tetratomidae	6	25
Ciidae	40	550
Melandryidae	80	450
Mordellidae	100	1200
Rhipiphoridae	35	400
Archaeocrypticidae	5	22
Pterogeniidae	2	8
Colydiidae	180	1300
Monommidae	12	225
Zopheridae	26	125
Perimylopidae	4	8
Chalcodryidae	4	6
Tenebrionidae	1700	18,000
Cephaloidae	7	20
Meloidae	120	3000
Oedemeridae	100	1000
Prostomidae	2	20
Synchroidae	2	10
Mycteridae	30	160
Boridae	2	5
Trichentomidae	2	15
Pythidae	16	50
Pyrochroidae	10	100
Salpingidae	42	350
Anthicidae	100	3000
Euglenidae	35	1100
Scraptiidae	30	400
Sf. Chrysomeloidea		
Cerambycidae	4000	35,000
Bruchidae	60	1500
Chrysomelidae	2500	35,000
Sf. Curculionoidea		
Nemonychidae	10	40
Anthribidae	325	2600
Oxycorynidae	8	30

Belidae	13	150
Ithyceridae	1	1
Aglycyderidae	3	160
Attelabidae	100	2100
Brentidae	325	2300
Apionidae	26	2200
Curculionidae	4500	50,000
(156 families)	25,100	340,600
STREPSIPTERA		
So. Mengenillidia		
Sf. Mengenilloidea		
Mengenillidae	3	7
So. Stylopidia		
Sf. Mengeoidea		
Corioxenidae	4	10
Sf. Bohartilloidea		
Bohartillidae	1	1
Sf. Halictophagoidea		
Halictophagidae	5	75
Sf. Stylopoidea		
Elenchidae	4	20
Myrmecolacidae	4	60
Stylopidae	9	200+
(7 families)	30	370
MECOPTERA		
So. Eumecoptera		
Meropeidae	2	2
Notiothaumidae	1	1
So. Eumecoptera		
Choristidae	3	8
Nannochoristidae	2	4
Panorpidae	5	300
Bittacidae	13	130
Apterobittacidae	1	1
So. Neomecoptera		
Boreidae	2	24
(8 families)	27	450
SIPHONAPTERA		
Sf. Hystrichopsylloidea		
Coptopsyllidae	1	23
Histrichopsyllidae	6	42
Stephanocircidae	8	51
Pygiopsyllidae	28	170
Ctenophthalmidae	41	630
Chimaeropsyllidae	8	28
Sf. Ceratophylloidea		
Ancistropsyllidae	1	3
Xiphiopsyllidae	1	8
Ceratophyllidae	68	760
Ischnopsyllidae	19	115
Sf. Malacopsylloidea		
Malacopsyllidae	2	2
Rhopalopsyllidae	11	150
Sf. Vermipsylloidea		
Vermipsyllidae	3	31
Sf. Pulicoidea		
Pulicidae	24	190
Tungidae	1	10
(15 families)	222	1700
DIPTERA		
So. Nematocera		
Sf. Tipuloidea		
Trichoceridae	6	110
Tipulidae	300+	13,000+
Sf. Psychodoidea		
Tanyderidae	11	37
Ptychopteridae	3	60
Psychodidae	45	500+
Sf. Culicoidea		
Dixidae	3	150
Chaoboridae	9	75
Culicidae	34	3000
Thaumaleidae	5	80
Simuliidae	60	1100
Ceratopogonidae	70	1200
Chironomidae	120	5000
Sf. Bibionoidea		
Perissosomatidae	1	5
Pachyneuridae	4	4
Axmyiidae	2	4
Anisopodidae	4	80
Bibionidae	15	700
Scatopsidae	15	200
Hyperoscelidae	4	12
Cecidomyiidae	600+	4000+
Sciaridae	50	500
Mycetophilidae	150	2000
Incertae Sedis		
Blepharoceridae	21	200
Deuterophlebiidae	1	7
Nymphiomyiidae	4	4
So. Brachycera		
Io. Orthorrhapha		
Sf. Tabanoidea		
Pelecorhynchidae	1	34
Rhagionidae	15	300
Anthericidae	7	100
Xylophagidae	10	100
Stratiomyidae	80	1400+
Tabanidae	130	3000+
Panthphthalmidae	3	25
Nemestrinidae	15	250
Acroceridae	45	450
Sf. Asiloidea		
Asilidae	400	5000
Mydidae	42	300
Therevidae	10	500
Scenopinidae	16	250+
Bombyliidae	200	4000+
Apioceridae	4	110
Sf. Empidoidea		
Empididae	100+	3000+
Dolichopodidae	150	6000
Io. Cyclorrhapha		
Div. Aschiza		
Sf. Lonchopteroidea		
Lonchopteridae	1	34
Sf. Phoroidea		
Platypezidae	20	100
Ironomyiidae	1	1
Sciadoceridae	2	2
Phoridae	220	2700
Sf. Syrphoidea		
Syrphidae	150	5000+
Pipunculidae	30	400
Div. Schizophora		
Sf. Conopoidea		
Conopidae	45	800
Sf. Tephritoidea		
Tephritidae	70+	4000
Otitidae	50	400
Platystomatidae	50	1000
Pyrgotidae	50	330
Tachiniscidae	3	3
Richariidae	31	160
Pallopteridae	8	50
Piophillidae	23	67
Lonchaeidae	8	500+
Sf. Micropezoidea		
Cypselosomatidae	2	3
Pseudopomyzidae	7	15
Neriidae	20	70
Micropezidae	40	420
Megamerinidae	4	11
Sf. Tanypezoidea		
Nothybiidae	1	9
Diopsidae	13	150
Tanypezidae	2	22
Psilidae	5	200
Syringogastridae	1	8
Strongylophthalmyiidae	1	30
Sf. Sciomyzoidea		
Heliomyzidae	4	14
Dryomyzidae	2	13
Coelopidae	7	20
Sciomyzidae	60	500
Chamaemyiidae	18	100
Ropalomeridae	9	30
Sepsidae	21	240

Lauxaniidae	130	1200+
Celyphidae	10	90
Sf. Opomyzoidea		
Opomyzidae	4	50
Clusiidae	22	200
Acartophthalmidae	1	2
Sf. Agromyzoidea		
Odiniidae	8	40
Agromyzidae	30	1800
Fergusoninidae	1	23
Sf. Asteioidea		
Neurochaetidae	1	3
Periscelidae	5	15
Teratomyzidae	2	20
Aulacigastridae	4	10
Asteiidae	10	100
Anthomyziidae	7	50
Rhinotoridae	3	12
Sf. Drosophiloidea		
Drosophilidae	40	1500
Mystacinobiidae	1	1
Camillidae	1	8
Ephydridae	70	1000+
Diastatidae	3	20
Curtonotidae	2	40
Sf. Chloropoidea		
Chloropidae	250	1000+
Milichiidae	19	300
Carnidae	4	40
Tethinidae	8	50
Canaceidae	10	60
Sf. Muscoidea		
Scatophagidae	50	250
Mormotomyiidae	1	1
Gasterophilidae	7	45
Anthomyiidae	50	1000
Muscidae	100	3000+
Calliphoridae	150	[5000]
Sarcophagidae	60	1400
Tachinidae	1000	6000+
Rhinophoridae	23	85
Cuterebridae	6	70
Oestridae	20	65
Glossinidae	1	22
Hippoboscidae	19	330
Streblidae	27	160
Nycterbiidae	10	200
Incertae Sedis		
Heleomyzidae	60	400+
Sphaeroceridae	56	700
Chyromyidae	4	35
Cryptochaetidae	1	20
Braulidae	1	4
(123 families)	6100	102,200

TRICHOPTERA		
Sf. Rhyacophiloidea		
Rhyacophilidae	2	450
Hydrobioscidae	40	150
Glossosomatidae	20	400
Hydroptilidae	75	600
Sf. Hydropsychoidea		
Philopotamidae	12	400
Stenopsychidae	3	70
Hydropsychidae	60	900+
Polycentropodidae	25	300
Dipseudopsidae	4	100
Ecnomidae	7	100
Psychomyiidae	15	150
Xiphocentronidae	4	20
Sf. Limnephiloidea		
Phryganeidae	15	70
Phryganopsychidae	1	3
Brachycentridae	10	100
Limnecentropodidae	1	10
Chathamiidae	2	4
Tasimiidae	4	6
Limnephilidae	130	1000
Goeridae	10	80
Thremmatidae	1	3
Uenoidae	4	25
Lepidosomatidae	30	250
Oeconesidae	6	15
Kokiriidae	6	7
Plectrotarsidae	3	5
Beraeidae	6	25
Sericosomatidae	25	100
Conoesucidae	13	30
Antipodoeciidae	1	1
Calocidae	4	10
Helicophidae	4	10
Molannidae	3	25
Odontoceridae	10	70
Atriplectridae	2	2
Philorheithridae	9	20
Helicopsychidae	6	100
Calamoceratidae	6	100
Leptoceridae	50	800
(39 families)	650	6500
LEPIDOPTERA		
So. Zeugloptera		
Sf. Micropterygoidea		
Heterobathmiidae	1	3
Micropterygidae	7	97
So. Dacnonympha		
Sf. Agathiphagoidea		
Agathiphagidae	1	2

Sf. Eriocranoidea		
Eriocraniidae	5	20
Lophocoronidae	1	3
Acanthopteroctetidae	1	5
Sf. Neopseustoidea		
Neopseustidae	3	7
So. Exoporia		
Sf. Mnesarchaeoidea		
Mnesarchidae	1	6
Sf. Hepialoidea		
Prototheoridae	2	7
Neotheoridae	1	1
Anomosetidae	1	1
Palaeosetidae	3	3
Palaeophatidae	1	1
Hepialidae	80	500
So. Monotrysia		
Sf. Nepticuloidea		
Nepticulidae	12	400
Opostegidae	1	50
Tischeriidae	1	65
Sf. Incurvarioidea		
Incurvariidae	27	340
Heliozelidae	9	100
So. Ditrysia		
Sf. Tineoidea		
Tineidae	300	3000
Acrolophidae	1	100
Psychidae	100	6000
Pseudarbelidae	3	6
Eriocottidae	3	60
Arhennophanidae	3	6
Ochsenheimeriidae	1	23
Phyllocnistidae	1	100
Gracillariidae	65	1000+
Lyonetiidae	12	300
Sf. Gelechioidea		
Oecophoridae	400	4000+
Ethmiidae	1	240
Stenomatidae	30+	700
Xylorictidae	40	500+
Stathmopodidae	9	175
Pterolonchiidae	1	10
Coleophoridae	6	500
Blastobasidae	10	100
Symmocidae	30	150
Elachistidae	30	200
Coelopoetidae	1	1
Batracheidae	4	125
Momphidae	1	80
Blastodacnidae	13	25
Selechiidae	500	4000+
Scythrididae	35	100+

Agonoxenidae	1	4
Cosmopterygidae	30+	1200
Sf. Alucitoidea		
Copromorphidae	6	40
Carposinidae	25	200
Alucitidae	5	50
Epermeniidae	6	71
Glyphipterigidae	3+	250
Sf. Yponomeutoidea		
Yponomeutidae	26+	1000
Amphitheridae	7	—
Argyesthiidae	2	100+
Douglasiidae	3	20
Acrolepiidae	3	70
Heliodinidae	70	350
Schreckensteiniidae	1	5
Sf. Sesioidea		
Choreutidae	40	400
Sesiidae	50	1000
Sf. Immoidea		
Immidae	1	150
Sf. Cossoidea		
Cossidae	100	1000
Metarbelidae	16	100
Dudgeoneidae	4	10
Sf. Tortricoidea		
Tortricidae	500	4000
Cochylidae	30+	500
Sf. Zygaenoidea		
Heterogynidae	1	5
Zygaenidae	50	300
Chrysopolomidae	3	20+
Somabrachyidae	1	3
Megalopygidae	20	220
Limacodidae	200	800+
Dalceridae	14	60+
Epipyropidae	6	20
Cyclotornidae	1	5
Sf. Castnioidea		
Castniidae	4	150
Sf. Hesperoidea		
Hesperiidae	500	3000+
Megathymidae	5	50
Sf. Papilionoidea		
Papilionidae	25	500+
Pieridae	70	2000
Lycaenidae	300	3000
Riodinidae	100+	1000+
Libytheidae	2	10
Ithomiidae	45	500
Danaidae	8+	200+
Satyridae	400	3000
Brassolidae	11	80
Morphidae	1	30
Amathusiidae	16	100+
Nymphalidae	200	4000
Acraeidae	6	225
Sf. Pterophoroidea		
Pterophoridae	50	500
Tineodidae	7	10
Oxychirotidae	2	5
Sf. Pyraloidea		
Thyrididae	100	600
Hyblaeidae	2	20
Pyralidae	1500	20,000
Sf. Drepanoidea		
Thyatiridae	50	200
Drepanidae	60	400
Sf. Geometroidea		
Geometridae	1500+	20,000+
Apoprogonidae	1	1
Epiplemidae	25	600
Sematuridae	5	40
Axiidae	2	5
Uraniidae	15	50+
Epicopeiidae	1	10+
Sf. Calliduloidea		
Callidulidae	8	100
Pterothysanidae	4	10
Sf. Mimallonoidea		
Mimallonidae	26	200
Sf. Bombycoidea		
Apatelodidae	17	250
Bombycidae	15	100
Eupterotidae	50	400
Anthelidae	8	75+
Brahmaeidae	7	20
Lasiocampidae	150	1500
Endromidae	1	1
Lemoniidae	3	15
Ratardidae	2	9
Carthaeidae	1	1
Oxytenidae	3	34
Cercophanidae	4	10
Saturniidae	100	1000
Sf. Sphingoidea		
Sphingidae	190	850
Sf. Noctuoidea		
Dioptidae	40	500
Thyretidae	25	200
Notodontidae	650	2000+
Thaumetopoeidae	23	120
Lymantriidae	200	2500
Arctiidae	250	2000+
Lithosiidae	300+	2000
Ctenuchidae	200	2000+
Pericopidae	30	300+
Hypsidae	15	100
Nolidae	15	250
Noctuidae	4000	25,000
Agaristidae	100	300
Cocytiidae	2	3
(138 families)	14,400	137,200
HYMENOPTERA		
So. Symphyta		
Sf. Megalodontoidea		
Xyelidae	5	50
Megalodontidae	3	45
Pamphilidae	6	170
Sf. Tenthredinoidea		
Cimbicidae	20	140
Tenthredinidae	150+	3000+
Argidae	50	500+
Blasticotomidae	1	4+
Pergidae	50	300+
Diprionidae	7	75
Sf. Siricoidea		
Xiphdriidae	22	90
Syntexidae	1	1
Siricidae	8	90
Orussidae	15	75
Sf. Cephoidea		
Cephidae	10	100
So. Apocrita		
Div. Parasitica		
Sf. Ichneumonoidea		
Braconidae	1400	37,500
Aphidiidae	35	350
Ichneumonidae	1200	15,000
Agriotypidae	1	3
Apozygidae	1	1
Sf. Trigonaloidea		
Trigonalidae	20	100
Sf. Megalyroidea		
Megalyridae	5	100
Stephanidae	7	100+
Sf. Evanioidea		
Evaniidae	12	500
Gasteruptiidae	10	500
Aulacidae	15	250+
Sf. Proctotrupoidea		
Pelecinidae	1	1
Monomachidae	2	12
Proctotrupidae	24	250
Heloridae	1	9
Roproniidae	1	8
Vanhorniidae	1	1
Austroniidae	1	3
Diapriidae	150	1200+
Sclelionidae	125	360+
Platygasteridae	50	400

Sf. Ceraphronoidea		
Ceraphronidae	12	150+
Megaspilidae	10	250+
Sf. Chalcidoidea		
Chalcidae	115	1400+
Leucopsidae	4	123
Eurytomidae	70	1100
Torymidae	100	1000
Agaonidae	12	160
Pteromalidae	565	2800
Perilampidae	25	200+
Eucharitidae	55	330
Eupelmidae	60	700+
Ormyridae	3	50
Encyrtidae	500+	2800
Tanaostigmatidae	14	33
Aphelinidae	42	800+
Signiphoridae	6	75
Tetracampidae	13	35
Elasmidae	8	220
Eulophidae	323	3000
Trichogrammatidae	70	440
Mymaridae	95	1200
Sf. Cynipoidea		
Ibaliidae	1	14
Liopteridae	13	65
Figitidae	30	250
Cynipidae	70	1200+
Div. Aculeata		
Sf. Chrysidoidea		
Plumariidae	5	20
Chrysididae	45	3000
Dryinidae	60	700
Eubolemidae	3	10
Sclerogibbidae	3	18
Scolebythidae	3	3
Bethylidae	80	2000
Loboscelidiidae	2	20
Sf. Tiphioidea		
Tiphiidae	100	1500
Sapygidae	9	85
Mutillidae	150	5000
Sierolomorphidae	1	10
Bradynobaenidae	6	200+
Sf. Pompiloidea		
Rhopalosomatidae	6	23
Pompilidae	150	2500
Sf. Formicoidea		
Formicidae	240	14,000
Sf. Scolioidea		
Scoliidae	20	300+
Sf. Vespoidea		
Masaridae	19	230
Eumenidae	120+	3000
Vespidae	36	800+
Sf. Sphecoidea		
Sphecidae	226	7700
Sf. Apoidea		
Colletidae	45	3000+
Halictidae	60	5000+
Andrenidae	20	4000+
Oxaeidae	4	20
Melittidae	12	700
Megachilidae	95	3000+
Anthophoridae	170+	4000+
Apidae	13	1000
(89 families)	7300	141,100

Total Insect Diversity
Families:. 997
Genera:. 73,000
Species: . . . 876,200

SOURCES. Protura: Janetschek (1970); Collembola: Salmon (1964); Diplura: Palct (1955), Richards & Davies (1977); Archaeognatha: Kugler (1982), Stura (1984); Thysanura: Kugler (1982); Ephemeroptera: Edmunds (1982); Odonata: Pinhey 1982, Davies & Tobin (1984,1985); Blattodea: Roth (1982); Mantodea: Brown (1982a); Isoptera: Brown (1982b); Grylloblattodea: (Brown 1982c); Orthoptera: Kevan (1982a); Phasmatodea: Kevan (1982b); Dermaptera: Brown (1982d); Embioptera: Ross (1982); Plecoptera: Bauman (1982); Zoraptera: Arnett & Jacques (1985); Psocoptera: Smithers (1982); Anoplura: Kim (1982); Mallophaga: Hopkins & Clay (1952), Emerson (1982); Thysanoptera: Stannard (1982); Hemiptera: Slater (1982); Homoptera: Kosztarab (1982); Megaloptera: Henry (1982); Raphidioptera: Henry (1982); Planipennia: Henry (1982); Coleoptera: Lawrence (1982,1987), Sen Gupta and Crowson (1966,1969); Strepsiptera: Brown (1982e); Mecoptera: (Brown 1982f); Siphonaptera: Smit (1982); Diptera: Bickel (1982); Diptera-Scatophagidae: Vockeroth (1987c); Trichoptera: Wiggins (1982); Lepidoptera: Munroe (1982); Hymenoptera: Brown (1982g); Hymenoptera-Megalryidae: Hedquist (1967); Hymenoptera-Stephanidae: Elliott (1922); Hymenoptera-Scelionidae: Masner (1976).

NOTES:

1. Genera in families listed in the first column; species in genera listed in the second column.
2. Totals for orders and the class are known species, and in most cases this is synonymous with described species. Values with many known but undescribed species are in brackets.
3. Those values for species and genera greater than a few dozen are mostly rounded off to the nearest ten (smaller values) or hundred (larger values). Ordinal totals for genera and species are also rounded, where appropriate.
4. Species breakdosns for families of Mantodea are currently unavailable.

APPENDIX E

REGISTER AND DETAILS OF FOSSIL INSECT LOCALITIES REFERRED TO IN THIS STUDY[1]

No.	*Locality*	*Lithostratigraphy*	*Fossil lithology*	*Epoch/ Period*	*Stage*	*Absolute Age (MYA)*	*References*
1 *	Lava Camp Mine Inmachuk River, Alaska	Imuruk Volcanics	Alluvial conglomerate	Late Miocene	Messinian	5.7	Hopkins *et al.* 1971
2 *	Randecker Maar, Swabia, FRG	Dysodile beds	Mudstone compressions	Late Miocene	Tortonian to Messinian	11.3-5.1	Geyer & Gwinner 1979; Schwaller 1986; Naumann 1987
3 **	Oeningen, near Baden, Switzerland	?	Laminated marl compressions	Late Miocene	Tortonian	11.3-6.1	Heer 1847, 1865; Handlirsch 1906/08; Zeuner 1939
4 *	Yermo, Calico Mtns., California, USA	Barstow Fm.	Mineral-replaced steinkerns	Middle to Late Miocene	Late Langhian to Messinian	14.4-5.1	Palmer 1957; Pierce 1966
5 **	Radaboj, Croatia, Yugoslavia	?	Laminated limestone compressions	Early Miocene	Burdigalian	19-?15	Heer 1847, 1865; Handlirsch 1906/08; Zeuner 1939
6 **	Bitterfeld, Saxony, DDR	"Blauen Erde"	Amber from the conifer *Cupressospermum*	Early Miocene	Aquatanian to Early Langhian	24.5-14.5	Barthel & Hetzer 1982; Schumann 1984; Schumann & Wendt 1989
7 *	Böttingen, Swabia, FRG	Böttingen Marble	Calcareous thermal sinter (hot springs)	Early Miocene	Aquatanian to Early Langhian	24.5-14.5	Zeuner 1927, 1929, 1931, 1939
8 **	Rott & Orsberg, Bavaria, FRG	Braunkohle	Laminated lignitic compressions	Early Miocene	Aquitanian	24.5-19	Handlirsch 1906/08; Zeuner 1939
9 *	Mainz-Kastel, Hessen, FRG	Hydrobia Limestone	Limestone compressions	Early Miocene	Aquitanian	24.5-19	Schmidtgen 1938; Zeuner 1938, 1939

---

[1] Asterisks below the deposit number indicate the relative importance of the fossil insect deposit: * = a minor deposit; ** = a deposit with a diversity of several orders; *** = a major deposit with substantial ordinal diversity. Nomenclature designating the period, epoch, stage and absolute age (in millions of years before the present) is from Harland *et al.* 1982.

No.	*Locality*	*Lithostratigraphy*	*Fossil Lithology*	*Epoch/ Period*	*Stage*	*Absolute Age (MYA)*	*References*
10 **	Creede, SW Colorado, USA	Creede Fm.	Tuffite	Latest Oligocene	Chattian	32.8-24.6	Carpenter *et al.* 1938; Cuffey *et al.* 1982
11 **	Simojovel, Chiapas, Mexico	Simojovel Fm.	Amber, probably from the legume Hymenaea	Late Oligocene /Early Miocene	Chattian/ Aquitanian	24.6-23.0	Hurd, Smith & Durham 1962; Langenheim 1964
12 *	Amagu, Kudia River, Siberia, USSR	?	Mudstone compressions	Late Oligocene /Early Miocene	Chattian/ Aquitanian	24.6-23.0	Cockerell 1925a
13 **	Cereste, Aix-en-Provence, France	?	Shale	Late Oligocene	Chattian	32.8-24.6	Théobald 1937
14 *	Camoins, Marseilles Basin, France	?	Limestone impressions	Early Oligocene	Rupelian	38-33	Timon-David 1943
15 ***	Florissant, Colorado, USA	Antero Fm., "Florissant lake beds"	Tuffite compressions	Early Oligocene	Rupelian	38-33	Durden 1966; Wilson 1978a
16 *	Mulhouse, Alsace, France	Formation Salifère	Saliferous shale compressions	Early Oligocene	Rupelian	38-33	Priesner & Quievreux 1935
17 ***	Cordillera Septentrional & Oriental, Dominican Republic	El Mamey Fm.	Amber, probably from the legume Hymenaea	Late Eocene to Early Miocene	Priabonian to Aquitanian	42-?20	Sanderson & Farr 1960; Kinzelbach 1979, 1983; Baroni-Urbani & Saunders 1982
18 **	Gurnard Bay, Isle of Wight, England	Bembridge Marl, "Insect Limestone"	Argillaceous limestone	Late Eocene/ Early Oligocene	Priabonian to Rupelian	42-32	Zeuner 1939; Jarzembowski 1976, 1980
19 ***	Baltic Region: Denmark, N. Germany & Poland; USSR Baltic Republics	Various formations; also in alluvial and glacial deposits	Amber, mostly of araucariaceous origin	Middle Eocene to Early Oligocene	Lutetian to Rupelian	50-32	Zeuner 1939; Larsson 1978; Keilbach 1982a, 1982b; Mills *et al.* 1985
20 *	Rio Limay, Neuquen Province, Argentina	Ventana Fm.	Tuffaceous siltstones and mudstones	Late Eocene	Bartonian	46-42	De Garcia 1983
21 *	Waikato, New Zealand	Papakaio Fm.	Compressions (?) in coal	Late Eocene	Bartonian	46-42	Harris 1984

No.	Locality	Lithostratigraphy	Fossil Lithology	Epoch Period	Stage	Absolute Age (MYA)	References
22 **	Seiseltales, Halle-an-der Salle, DDR	Braunkohle	Original cuticle in coaliferous sediment	Middle Eocene	Lutetian to Bartonian	50.5-42	Voigt 1938; Zeuner 1939; Haupt 1950; Kinzelbach & Lutz 1985
23 **	SW Wyoming, NW Colorado & NE Utah, USA	Green River Fm.	Shale compressions	Middle Eocene	Lutetian to Bartonian	50.5-42	Wilson 1978a; Grande 1980
24 *	Grube Messel, Frankfurt-au-Main, FRG	Messel Fm.	Oil shale compressions	Middle Eocene	Lutetian	50.5-?46	Straus 1976; Franzen 1985; Lutz 1987
25 *	Lower Mississippi Valley, USA	Wilcox and Claiborne Fms.	Amber, of *Shorea* origin; insect damage on leaf compressions	Early to Middle Eocene	Ypresian to Bartonian	55-42	Brooks 1955; Saunders *et al.* 1974
26 *	Bognor Regis, Sussex, England	London Clay	Pyrite	Early Eocene	Ypresian	55-50.5	Britton 1960; Venables & Taylor 1962; Jarzembowski 1986
27 **	Menat, Auvergne Region, France	?	Compressions in tuffaceous shales	Early Eocene	Ypresian	55-50.5	Handlirsch 1908; Piton 1940
28 *	Sheridan Pass area, Wyoming, USA	Upper Wind River Fm.	Leaf mine on a *Cedrela* impression in tuffaceous shale	Early Eocene	Early Ypresian	55-53	Hickey & Hodges 1975; Crane & Jarzembowski 1980
29 *	Cold Ash Quarry, southern England	Reading Beds	Leaf mines on angiosperm compressions	Late Paleocene	Thanetian	60-55	Crane & Jarzembowski 1980
30 *	Bundamba, SW Queensland, Australia	Redbank Plains Fm.	Impressions in clay ironstones	Paleocene	[unassigned]	65-55	Day *et al.* 1983; Lambkin 1987
31 *	Yushangou, Kavalenow District; Maritime Territory, USSR	Tadushi Suite	Shale impressions	Paleocene	[unassigned]	65-55	Ponomarenko & Rasnitsyn 1974
32 *	Blackfolds and Joffre, Alberta, Canada	Paskapoo Fm.	Shale compressions	Paleocene	Danian	65-62	Wilson 1978a; Kevan & Wighton 1981
33 *	Seminar Hills, Nagpur, India	Intertrappean Series	Original(?) chitin preserved 3-D in limey clay	Late Cretaceous	Late Maastrichtian	66-65	George 1952

No.	Locality	Lithostratigraphy	Fossil Lithology	Epoch/ Period	Stage	Absolute Age (MYA)	References
34 *	Fossil Forest, San Juan Basin, New Mexico, USA	Fruitland Fm.	Larval cases in sandstone	Late Cretaceous	Campanian-Maastrichtian	78-65	Wolberg *et al.* 1988
35 ***	Medicine Hat, Cedar Lake, Manitoba, Canada	Belly River Series, Foremost Fm.	Amber, probably of taxodiaceous origin	Late Cretaceous	Campanian	78-73	Walker 1934; Carpenter et al. 1937; McAlpine & Martin 1969
36 *	Kinkora, east-central New Jersey, USA	Magothy Fm.	Amber, probably of araucariaceous origin, in lignite	Late Cretaceous	?Campanian	83-73	Langenheim & Beck 1968; Grimaldi 1988; Grimaldi et al. 1989
37 ***	Jantardach eastern Taimyr Peninsula, Siberia, USSR USSR	Kheta Fm.	Amber	Late Cretaceous	Coniacian to Late Santonian	88.5-86	Zherichin & Sukacheva 1973; Evans 1973; Skalski 1979b
38 *	Raritan Bay, New Jersey, USA	Magothy Fm.	Amber, probably of taxodiaceous origin, in claystone	Late Cretaceous	Turonian to Coniacian	91-87.5	Wilson *et al.* 1967a 1967b; Brown 1969; Grimaldi et al. 1989
39 **	Kizyl-Zhar, Karatau Range, Kazakstan, USSR	?	Shale compressions	Late Cretaceous	Turonian	91-81.5	Sharov 1971; Rasnitsyn 1975; Kozlov 1988
40 *	Kaolak, Ketik & Kuk River valleys, N coastal plain, Alaska, USA	Prince Creek Fm., Chandler Fm.	Amber, probably of taxodiaceous origin, in coaliferous sediments	Late Cretaceous	?Cenomanian to Santonian	?97.5-83	Langenheim *et al.* 1960; McAlpine & Martin 1969
41 *	New Ulm, Minnesota, USA	Windrow Fm., Ostrander Member	Claystone compression	Late Cretaceous	Cenomanian to Turonian	97.5-88.5	Lewis 1970; Shields 1989
42 **	Agapa, eastern Taimyr Peninsula, Siberia USSR	Dolganian Suite	Amber	Late Cretaceous	Late Cenomanian	95-91	Remm 1976
43 *	Orapa, Francistown, central Botswana	Unnamed basin sediments associated with kimberlite pipe	Mudstone impressions and compressions	Late Cretaceous	Cenomanian	93.0	McKay & Rayner 1986; Rayner 1987; Waters 1989a, 1989b

No.	Locality	Lithostratigraphy	Fossil Lithology	Epoch/ Period	Stage	Absolute Age (MYA)	References
44 *	Bohemia, Czechoslovakia	"Perucer Schichten"	Leaf mines and insect damage on leaf compressions	Late Cretaceous	Cenomanian	97.5-91	Fritsch 1882; Fric 1901; Handlirsch 1906/08
45 **	Bezonnais & Durtal, NW France	?Cambridge Greensand	Amber, of araucariaceous origin, in black claystone	Late Cretaceous	Cenomanian	97.5-91	Kühne, Kubig & Schlüter 1973; Schlüter 1975, 1978
46 **	Magadan, Arman River, NE Siberia, USSR	Olskaya Suite	Shale(?) compressions	Late Cretaceous	Cenomanian	97.5-91	Kormilev & Popov 1986
47 *	Schefferville, near Knob Lake, Labrador, Canada	Redmond Fm.	Ferruginous shale compression	Late Cretaceous	Cenomanian	97.5-91	Dorf 1967; Emerson 1967
48 *	Hardin Co., Tennessee, USA	?	Amber	Late Cretaceous	[unassigned]	97.5-65	Ross 1958; Langenheim 1969; Botosaneanu & Wichard 1984
49 *	Stump Neck, Maryland, USA	Potomac Gp., Patapsco Fm.	Leaf galls on angiosperm compressions	Early Cretaceous	Late Albian	105-98	Hickey and Doyle 1977
50 *	Dupree, South Dakota; Kansas & Nebraska; USA	Fox Hills Fm.	Concretion, in sandy shale; galls & mines on leaf compressions	Early/Late Cretaceous	?Albian to Cenomanian	?113-91	Hagen 1882; Northrup 1928
51 *	Yukhary, Agdzhakend, Shaymayanovsk, Dist., Azerbaydzhanian SSR, USSR	"Copal-containing Suite"	Amber	Early Cretaceous	Aptian to Cenomanian	119-91	Rasnitsyn 1977a
52 **	Baisa & Unda, Vitim Creek, Transbaikalia, Buryat ASSR, USSR	Zazinskaya Fm., Baisinsk Stratum	Mudstone and marl compressions; tuffite	Early Cretaceous	Aptian to Albian	119-97.5	Sukacheva 1968, Rasnitsyn 1969; Zherikin 1978; Krassilov & & Rasnitsyn 1982
53 **	South Gippsland, Victoria, Australia	Korumburra Gp., Koonwarra Fossil Bed	Claystone compressions	Early Cretaceous	Late Aptian	115-113	Drinnan & Chambers 1986; Dettmann 1986; Jell & Duncan 1986
54 *	Las Hoyas, Cuenca, Spain	La Huerguina Fm. Unit III	Laminated limestone	Early Cretaceous	Late Hauterivian	128-125	Sanz *et al.* 1988

No.	Locality	Lithostratigraphy	Fossil Lithology	Epoch/ Period	Stage	Absolute Age (MYA)	References
55 *	Jezzîne, southern Lebanon	"Grés de Base"	Amber of araucariaceous origin in lignite and sandstone	Early Cretaceous	Hauterivian to Aptian	131-113	Schlee & Dietrich 1970; Dietrich 1976; Whalley 1977, 1978
56 **	Montsech, Lerida, Spain	Caliza con Caráceas Fm.	Lithographic limestone compressions	Early Cretaceous	Late Berrasian to Early Valanginian	137-139	Garrido-Megias & Rios Aragdes 1972; Whalley & Jarzembowski 1985
57 *	Weald Region, southern England	Weald Clay, Waldhurst Clay, Fairlight Clay, "Durlston Fm."	Siltstone impressions	Early Cretaceous	Berraisian to Barremian	144-119	Edmunds & Gallois 1965; Jarzembowski 1984
58 *	Urtuya & Bolboia, Priarguisky Region, USSR	Bukunskay Suite	Siltstone compressions	Late Jurassic to Early Cretaceous	Tithonian to Berriasian	150-138	Kalugina 1989
59 *	Purbeck, Dorsetshire, England	Purbeck Limestone	Limestone impressions	Late Jurassic	Tithonian	147-144	Brodie 1845; Zeuner 1939
60 ***	Galkina & Mikhailovka, Karatau Range, Kazakhstan, USSR	Karabastausk Stratum	Shale compressions	Late Jurassic	Tithonian	150-144	Martynov 1926; Rodendorf *et al.* 1968; Rasnitsyn 1969; Crowson 1981; Hennig 1981
61 **	Langenaltheim, Solnhofen and Eichstätt, Bavaria, FRG	Solnhofen Fm., Upper Solnhofen Limestone Member	Lithographic limestone compressions	Late Jurassic	Early Tithonian	150-147	Zeuner 1939; Kuhn 1961; Barthel & Jablonski 1979; Sall 1983
62 *	Mogzon & Uda, Chita District, Transbaikalia, USSR	Udinskaya Fm., Bukukun Fm.	Shale compressions	Middle to Late Jurassic	Callovian-Oxfordian	169-156	Skoblo 1966, Kovalev 1982; Sinichenkova 1983; Kalugina & Kovalev 1985
63 *	Yorkshire, England	Lower Oolite Fm.	Insect damage on leaf compressions in mudstone	Middle Jurassic	Bajocian	181-175	Scott & Patterson 1984
64 **	Haifanggou, Liaoning Prov., and Jiulongshan, Hebei Prov.; China	Haifanggou Fm. and Jiulongshan Fm.	Claystone compressions	Middle Jurassic	Bajocian	181-175	Hong 1983

No.	*Locality*	*Lithostratigraphy*	*Fossil Lithology*	*Epoch/ Period*	*Stage*	*Absolute Age (MYA)*	*References*
65 *	Kubekovo, Krasnoyarsk Region, USSR	Itat Fm.	Shale compressions	Middle Jurassic	[unassigned]	188-163	Sharov 1971; Sinichenkova 1985; Gorochov 1988
66 **	Novospasskoye, Nova Bryansk, Transbaikalia, Buryat ASSR, USSR	Ichetaya Fm.	Shale compressions	Early to Middle Jurassic	Toarcian to Aalenian	194-181	Kovalev 1981, 1982
67 **	Ust-Balei & Iya, Angara River, Irkutsk Region, USSR	Chevemkhovsk Series, Prisayansk Stratum	Shale compressions	Early Jurassic	Pliensbachian or Toarcian	200-188	Brauer, Redtenbacher & Ganglbauer 1889; Rasnitsyn 1969; Sharov 1971; Hennig 1981
68 *	Mecklenburg & Dobbertin, Rostock, DDR	"Posidonienschiefer" or lateral equivalent	Shale compressions	Early Jurassic	Pliensbachian or Toarcian	200-188	Handlirsch 1939; Zeuner 1939; Bode 1953
69 **	Gloucestershire, Dorset, Warwickshire, & Worchestershire, England	Lower Lias "Flatstone"	Calcareous mudstone compressions	Early Jurassic	Sinemurian	206-200	Brodie 1845; Tillyard 1933; Zeuner 1962; Cope *et al.* 1981; Whalley 1985
70 **	Kizyl-Kiya Oshsk Region, Kirghiz SSR, USSR	Stratum N	Mudstone compressions	Early Jurassic	probably Sinemurian	206-200	Martynov 1937a; Rasnitsyn 1969; Sukacheva 1973
71 *	Shurab & Kisyl-kiya, Isafara District, Tadzhikstan, USSR	Shurab Suite, Series A, B, E, H, R & Z	Shale compressions	Early Jurassic	Sinemurian or Hettangian	213-200	Martynov 1937a; Crowson *et al.* 1967
72 *	Schaabelen, Aargau, Switzerland	?	Shale compressions	Early Jurassic	Hettangian	213-206	Heer 1865; Handlirsch 1906/1908
73 **	Issyk-Kul, Soguta, Tomsk Region, Kirghiz SSR, USSR	Dzhil'sk Fm.	Mudstone compressions	Late Triassic to Early Jurassic	Rhaetian to Hettangian	219-206	Martynov 1937a; Rasnitsyn 1969; Sharov 1971; Hennig 1981; Gorochov 1988
74 **	Denmark Hill, (Ipswich), Queensland, Australia	Ipswich Series, Blackstone Fm., Ipswich Insect Bed	Mudstone compressions	Late Triassic	Rhaetian	219-213	Tillyard 1923c; Dunstan 1924, Tindale 1945

No.	*Locality*	*Lithostratigraphy*	*Fossil Lithology*	*Epoch/ Period*	*Stage*	*Absolute Age (MYA)*	*References*
75 *	Botswana and Transvaal, South Africa	Stormberg Series, Cave Sandstone	(?) Shale impressions	Late Triassic	Rhaetian	219-213	Haughton 1924; Zeuner 1939
76 *	Virginia & North Carolina, USA	Dan River Gp., Cow Branch Fm.	Microlaminated siltstone	Late Triassic	Carnian	231-225	Olsen et *al.* 1978
77 *	Holbrook, Arizona, USA	Chinle Fm.	Borings in petrified araucariaceous wood	Late Triassic	[unassigned]	231-213	Walker 1938
78 **	Bird's River, Natal, South Africa	Molteno Fm.	Shale compressions	Late Triassic	[unassigned]	231-213	Zeuner 1939; Riek 1974, 1975, 1976
79 **	Mt. Crosby & Dinmore, Queensland, Australia	Ipswich Series, Blackstone Fm., Mt. Crosby Insect Bed	Mudstone compressions	Late Triassic	Carnian	231-225	Tindale 1945; Riek 1955; Rasnitsyn 1969; Rozefelds & Sobbe 1987
80 **	Beacon Hill & Brookvale, New South Wales, Australia	Hawkesbury Sandstone Series	Shale compressions	Middle Triassic	[unassigned]	243-231	Riek 1950
81 *	Saverne & Sarre-Union, Vosges, NE France	Grès à Voltzia	Shale compressions	Early Triassic	Smithian or Spathian	245-243	Hennig 1981; Gall 1983
82 **	Dzhailyaucho, Madygen, Turkestan Range, western Kirgizia, USSR	Upper Madygenskaya Suite	Claystone compressions	Early Triassic	[unassigned]	248-243	Rasnitsyn 1969; Sukacheva 1973
83 **	Belmont & Warner's Bay, New South Wales, Australia	Newcastle Coal Measures	Chert	Late Permian	Tatarian	253-248	Tillyard 1926b; Knight 1950; Wootton 1981
84 *	Mooi River, Karoo Basin, Natal, South Africa	Middle Beaufort Series, *Daptocephalus* Zone	Shale compressions	Late Permian	[unassigned]	258-248	Riek 1973

No.	*Locality*	*Lithostratigraphy*	*Fossil Lithology*	*Epoch/ Period*	*Stage*	*Absolute Age (MYA)*	*References*
85 *	Brodie Creek Head, Malvinas/ Falklands, Argentina/UK	"Bodie Creek Beds"	Chert	Late Permian	[unassigned]	258-248	Tillyard 1928c
86 **	Iva Gora, Sheimo Gora, & Letopala; Soyana River; Arkangelsk Region, USSR	?	Shale compressions	Late Permian	Kazanian	?255-253	Martynov 1928, 1938a; Rohdendorf 1957; Sharov 1971
87 *	Kargala, Perm Region, USSR	Mine tailings	Shale compressions	Late Permian	Kazanian	?255-253	Zalessky 1933; Martynov 1937b
88 **	Tikhie Sory, Kama River, Tatar ASSR, USSR	?	Shale compressions	Late Permian	Kazanian	?255-253	Martynov 1938a; Rohdendorf 1957
89 **	Chekarda, southern Urals, USSR	?	Siltstone compressions	Early Permian	Kungurian	263-258	Sharov 1971; Hennig 1981
90 ***	Elmo, Kansas, & Noble Co., Oklahoma, USA	Wellington Fm., Elmo Limestone & Midco Members	Siltstone compressions	Early Permian	Artinskian	268-263	Dunbar & Tillyard 1924; Carpenter 1930; 1930b; Tasch & Zimmerman 1959, 1962
91 *	Hammanskraal, Transvaal, South Africa	Middle Ecca Series	Carbonaceous shale compressions	Early Permian	[unassigned]	286-258	Riek 1976a,1976b; [?Plumstead 1963]
92 *	Obora, Boskovice Furrow, Moravia, Czechoslovakia	?	Slate compressions	Early Permian to Late Carboniferous	Artinskian to Gzelian	291-263	Kukalova 1963, 1968; Crowson et al. 1967; Durden 1984
93 *	Tunguska Basin, Krasnoyarsk Region, USSR	Burgukli Series	Shale compressions	Early Permian to Late Carboniferous	Artinskian to Szelian	291-263	Martynova 1961; Crowson et al. 1967
94 **	Gotha, Thuringia, DDR	Rothliegende Series	Shale compressions	Early Permian to Late Carboniferous	Artinskian to Early Moscovian	305-263	Guthörl 1934; Staeske 1963; Müller 1975
95 **	Commentry, central France	Grand Couche	Shale compressions	Late Carboniferous	Gzelian	291-286	Stevenson 1910; Carpenter 1963

No.	Locality	Lithostratigraphy	Fossil Lithology	Epoch/ Period	Stage	Absolute Age (MYA)	References
96 ***	Mazon Creek, Illinois, USA	Carbondale Fm., Francis Creek Shale Member	Siderite nodules	Late Carboniferous	Late Moscovian	298-294	Handlirsch 1911; Richardson 1956; Baird 1979; Baird *et al.* 1985a, 1985b
97 ***	Kusnetsk, Kemerov District, Siberia, USSR	Upper and Lower Balakhonkian Suites	Shale compressions	Late Carboniferous/Early Permian	?Bashirskian to Sakmarian	?310-268	Rodendorf *et al.* 1961; Wootton 1981; Durden 1984
98 *	Horní Suchá, Upper Silesian Coal Basin, Czechoslovakia	"Coal Measures," Coal Seam 31	Mudstone compressions	Late Carboniferous	Yeadonian	318-315	Kukalová 1958, 1964; Hennig 1981
99 **	Hagen-Vorhalle, Ruhr Region, FRG	Vorhalle Beds	Mudstone impressions	Late Carboniferous	Early Bashkirian	318-316	Brauckmann 1988
100 *	Gulpen, South Limburg, Holland	?Millstone Grit	Coalified impressions	Late Carboniferous	Early Bashkirian	318-316	Pruvost 1927; Laurentiaux 1950; Brauckmann 1988
101 *	Charleroi Coal Basin, Belgium	"Terrain Houillier"	Shale compressions	Late Carboniferous	Early Bashkirian	318-316	Laurentiaux-Vieira & Laurentiaux 1985; Brauckmann 1988
102 *	Gilboa, New York, USA	Panther Mountain Fm.	Unaltered cuticle in in a black mudstone	Middle Devonian	Middle Givetian	379-376	Shear *et al.* 1984, 1987; Norton *et al.* 1988
103 *	Gaspé, Québec, Canada	Battery Point Fm.	Unaltered cuticle in mudstone	Early Devonian	Early Emsian	392-390	Labandeira *et al.* 1988
104 *	Rhynie, Scotland	Old Red Sandstone	Chert	Early Devonian	Siegenian	401-394	Hirst & Maulik 1926; Tillyard 1928a; Tasch 1957

APPENDIX F

DOCUMENTATION OF FOSSIL HEXAPOD OCCURRENCES FOR MOUTHPART CLASS GEOCHRONOLOGY

MOUTHPART CLASS 1: ENTOGNATHATE

Fig. 31

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
1.	Archpolypoda: *Kampecaris* sp.	[Pridoli]	Almond 1985; Selden & Edwards 1989
2.	Campodeidae: *Campodea darwini* Silvestri	[19]	Silvestri 1912
3.	Testajapygidae: *Testajapyx thomasi* Kukalová-Peck	[96]	Kukalová-Peck 1987
4.	Japygidae: *Onchojapyx schmidti* Pierce	[Miocene]	Pierce 1950
5.	Isotomidae: *Rhyniella praecursor* Hirst & Maulik	[104]	Hirst & Maulik 1926; Greenslade 1986
6.	Entomobryidae: *Permobrya mirabilis* Riek	[91]	Riek 1976a
7.	Entomobryidae: *Protentomobrya walkeri* Folsom	[78]	Folsom 1937
8.	Isotomidae: *Isotoma crassicornis* Handschin, Hypogasturidae: *Hypogastura protoviatica* Handschin, Entomobryidae: *Orchesella eocaenica* Handschin	[19]	Handschin 1926c
9.	Isotomidae: *Cryptopygus* sp. (Mari Mutt), Entomobryidae: *Lepidocyrtus* sp. (Mari Mutt)	[17]	Mari Mutt 1983
10.	Isotomidae: *Isotomurus retardatus* Folsom, Entomobryidae: *Entomobrya ?trifasciata* Handschin	[11]	Christiansen 1971
11.	?Neanuridae: undescribed form	[104]	Greenslade 1988
12.	Poduridae: *Podura pulchra* Koch & Berendt	[19]	Koch & Berendt 1954; Keilbach 1982
13.	Smithurinidae: *Smithurinus brevicornis* Koch & Berendt	[19]	Koch & Berendt 1954; Keilbach 1982
14.	Smithurinidae: *Sphyrotheca* sp. (Mari Mutt)	[17]	Mari Mutt 1983

MOUTHPART CLASS 2: MONOCONDYLATE

Fig. 34

1.	Testajapygidae: *Testajapyx thomasi* Kukalová-Peck	[96]	Kukalová-Peck 1987
2.	Campodeidae: *Campodea darwini* Silvestri	[19]	Silvestri 1912; Larsson 1978
3.	Japygidae: *Onychojapyx schmidti* Pierce	[4]	Redell 1983
4.	Meinertellidae: *?Neomachilellus* sp. Wygodzinsky	[11]	Wygodzinsky 1971
5.	?Machilidae: undescribed fragments	[102]	Shear *et al.* 1984
6.	Machilidae: undescribed forms	[96]	Kukalová-Peck 1988, pers. comm.
7.	?Machilidae: undescribed forms	[37]	Zherikin & Sukacheva 1973
8.	Machilidae: *Machilis diastatica*	[19]	Olfers 1908; Larsson 1978
9.	Machilidae: "Borstenschwänze"	[17]	Schlee & Glockner 1978
10.	Machilidae "Felsenspringer"	[7]	Schumann & Wendt 1989
11.	Palaeognathidae: *Gaspea palaeoectognathae* Labandeira, Beall & Hueber	[103]	Labandeira, Beall & Hueber 1988

MOUTHPART CLASS 3: ADULT ECTOGNATHATE

Fig. 37

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
1.	Palaeoectognathidae: *Palaeoectognatha gaspea* Labandeira, Beall & Hueber 1988	[104]	Labandeira, Beall & Huever 1988
2.	Dasyleptidae: "*Dasyleptus*" Kukalová-Peck 1987	[96]	Kukalová-Peck 1987
3.	Dasyleptidae: *Dasyleptus lucasi* Brongniart	[95]	Brongniart 1885
4.	Dasyleptidae: *Dasyleptus brongniarti* Sharov	[97]	Sharov 1966
5.	Dasyleptidae: *Lepidodasypus sharovi* Durden	[90]	Durden 1978
6.	Family uncited: "Felsenspringen"	[55]	Schlee 1972
7.	Lepismatidae	[37]	Zherikin & Sukacheva 1973
8.	Lepismatidae	[33]	George 1952
9.	Lepismatidae	[15]	Wilson 1978a
10.	Family uncited: "Felsenspringer"	[11]	Schlee & Glockner 1978
11.	Lepidothricidae: *Lepidothrix pilifera* Menge	[6]	Schumann & Wendt 1989
12.	Triplosobiidae: *Triplosoba pulchella* Brongniart	[95]	Brongniart 1893; Crowson *et al.* 1967
13.	Meganeuridae: *Namurotypus sippeli* Brauckmann & Zessin	[99]	Brauckmann and Zessin 1989
14.	Palaeoperlidae: *Palaeoperla exacta* Sharov, Palaeonemouridae: *Palaeonemoura altaica* Sharov	[97]	Sharov 1961
15.	Palaeoperlariidae: *Perlopsis filicornis* Martynov	[89]	Martynov 1940; Crowson *et al.* 1967
16.	?Leuctridae: *Permoleuctropsis gracilis* Martynov	[87]	Martynov 1937b
17.	?Gripopterygidae: *Euxenoperla simplex* Riek	[84]	Riek 1973
18.	Eustheniidae: *Stenoperlidium permianum* Tillyard	[83]	Tillyard 1935b
19.	Eustheniidae: *Mesonotoperla sinuata* Riek	[80]	Riek 1953b
20.	?Gripopterygidae: *Euxenoperla clara* Riek	[78]	Riek 1976b
21.	Eustheniidae: *Stenoperlidium triassicum* Riek	[74]	Riek 1956
22.	Taenopterygidae: *Mesotaeniopteryx elongata* Martynov., Mesoleuctridae: *Mesoleuctra exerta* Sinichenkova	[71]	Martynov 1937a; Sinichenkova 1987
23.	Mesoleuctridae: *Mesoleuctra gracilis* Sinichenkova, Platyperlidae: *Platyperla platypoda* Sinichenkova, Taeniopterygidae: *Mesonemoura maakii* Brauer, Redtenbacher & Ganglbauer 1889	[67]	Sinichenkova 1987; Brauer, Redtenbacher & Ganglbauer 1889; Illies 1965
24.	Siberioperlidae: *Siberioperla lacunosa* Sinichenkova	[66]	Sinichenkova 1987
25.	Nemouridae: *Rectonemoura yujiagouensis* Hong, Taeniopterygidae: *Sinotaenopteryx luanpingensis* Hong	[64]	Hong 1983
26.	Siberioperlidae: *Siberioperla bukukunica* Sinichen-	[62]	Sinichenkova 1987
27.	Baleyopterygidae: *Udopteryx expansa* Sinichenkova, Perlariopseidae	[60]	Sinichenkova 1987; Rasnitsyn 1988
28.	Gripopterygidae: *Eodinotoperla duncanae* Jell & Duncan	[53]	Jell & Duncan 1986
29.	Chloroperlariidae: *Dipsoperla serpentis* Sinichenkova, Perlariopseidae: *Accretonemoura grata* Sinichenkova, Baleiopterygidae: *Baissoleuctra irinae* Sinichenkova	[52]	Sinichenkova 1987; Rasnitsyn 1988

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
30.	Pteronarcyidae: *Palaeopteron complexus* Rice	[47]	Rice 1968
31.	Family undetermined	[37]	Zherikin & Sukacheva 1973
32.	Family undetermined	[24]	Lutz 1987
33.	Nemouridae: *Nemoura ocularis* Pictet, Perlidae: *Perla prisca* Pictet; Leuctriidae: *Leuctra linearis* Hagen, Taeniopterygidae: *Taeniopteryx elongata* Hagen, Perlodidae: *Perlodes resinata* (Hagen)	[19]	Pictet-Baraban & Hagen 1856; Larsson 1978
34.	Leuctriidae: *Leuctra priscula* (Cockerell)	[18]	Jarzembowski 1980
35.	?Leuctriidae, ?Capniidae	[6]	Schumann & Wendt 1989
36.	Taeniopterygidae: *Brachyptera schmiditi* Illies	[Pliocen]	Illies 1967
37.	Family uncertain: *Genentomum validum* Scudder, *Progenetomum carbonis* Handlirsch	[96]	Scudder 1885; Handlirsch 1908; Crowson et al. 1967
38.	Elcanidae: *Promartynovia venicosta* Sharov	[90]	Tillyard 1937; Zessin 1987
39.	Elcanidae: *Proelcana urlica* Sharov	[89]	Sharov 1962; Zessin 1987
40.	Elcanidae: *Promartynovia sojanense* Sharov	[86]	Sharov 1962; Zessin 1987
41.	Elcanidae: *Meselcana madygenica* Sharov	[82]	Sharov 1971 (1968); Zessin 1987
42.	Locustopsidae: *Triassolocusta leptoptera* Tillyard	[79]	Tillyard 1922; Crowson et al. 1967
43.	Haglidae: *Hagla contorta* Riek	[78]	Riek 1974
44.	Elcanidae: *Elcana geinitzi* Heer	[72]	Geinitz 1880; Zessin 1987
45.	Prophalangopsidae: *Archaboilus kisylkiensis* Martynov., Elcanidae: *Archelcana shurabica* Sharov	[71]	Martynov 1937a; Sharov 1971 (1968); Zessin 1987
46.	Triassomantidae: *Orichalcum ornatum* Whalley, Gryllidae: *Protogryllus magnus* Zeuner, Haglidae: *Protohagla langi* Zeuner, Elcanidae: *Archelcana durnovaria* Whalley, Locustopsidae: *Locustopsis spectabilis* Zeuner	[69]	Zeuner 1937, 1942, 1962; Whalley 1985
47.	Elcanidae: *Parelcana tenuis* Handlirsch, Haglidae: *Hagla*, sp.; Gryllidae: *Protogryllus hattorfensis* Bode, Locustopsidae: *Locustopsis maculosa* Bode	[68]	Handlirsch 1908; Bode 1953; Zessin 1987
48.	Isfaropteridae: *Isfaroptera yujiagouensis* Hong, Haglidae: *Sinoprophalangopsis reticulata* Hong, Elcanidae: *Elcana reticulata* Handlirsch	[64]	Handlirsch 1925; Hong 1983
49.	Gryllacrididae: *Jurassobatea gryllacroides* Zeuner, Prophalangopsidae: *Cyrtophyllites rogeri* Oppenheim, Elcanidae: *Elcana phyllophora* Handlirsch	[61]	Handlirsch 1908; Zeuner 1939
50.	Prophalangopsidae: *Pamphagopsis maculata* Martynov, Elcanidae: *Elcana minuta* Sharov	[60]	Zeuner 1939; Sharov 1971(1968); Zessin 1987
51.	Tettigoniidae: *Termitidium ignotum* Westwood, Prophalangopsidae: *Zalmona brodei* Giebel, Elcanidae: *Elcana tessellata* Westwood	[59]	Westwood 1854; Zeuner 1939; Zessin 1987
52.	Acridoidea, Elcanidae, Gryllidae, Prophalangopsidae	[57]	Jarzembowski 1984
53.	Tridactylid indet.; ?Gryllacridoid indet.	[53]	Jell and Duncan 1986
54.	Elcanidae: *Baisselcana sibirica* Sharov	[52]	Sharov 1971(1968); Zessin 1987; Rasnitsyn 1988
55.	Gryllidae	[43]	(McKay & Ratner 1986)
56.	Gryllidae, Locustopsidae	[39]	Rasnitsyn 1988
57.	Acrididae	[33]	(George 1952)

(ADULT ECTOGNATHATE, continued)

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
58.	Acrididae	[32]	Wilson 1978a
59.	?Gryllacrididae, Ensifera	[24]	Lutz 1987
60.	Tettigoniidae: *Tettigoniidarum* sp., Gryllidae, Acrididae	[23,22]	Zeuner 1939; Wilson 1978a
61.	Tetrigidae: *Succinotettix chopardi* Piton, Tettigoniidae: *Eomortoniellus handlirschi* Zeuner, Gryllacrididae: *Prorhaphidophora zeuneri* Chopard, Gryllidae: *Gryllulus* sp.	[19]	Zeuner 1936; Chopard 1936; Piton 1938; Keilbach 1982
62.	Gryllotalpidae: *Gryllotalpa prima* Cockerell	[18]	Zeuner 1939
63.	Tettigoniodea, Grylloidea	[17]	Schlee & Glockner 1978
64.	Gryllacrididae: *Palaeorehnia maculata* Cockerell;	[15,13]	Zeuner 1939; Wilson 1978a
65.	Gryllotalpidae: *Neocartella schmidtgeni* Zeuner	[9]	Zeuner 1937
66.	Acrididae: *Protocatantops gracilis* Zeuner, Gryllotalpidae: *Gryllotalpa miocaenica* Zeuner, Tettigoniidae: *Rammea laticeps* Zeuner, Gryllidae: aff. *Oecanthinarum*	[7]	Zeuner 1931
67.	Tettigoniidae, *sensu lato*, Grylloidea	[6]	Schumann & Wendt 1989
68.	Tettigoniidae: *Platycles speciosa* Heer	[3]	Heer 1865; Zeuner 1939
69.	Geinitziidae: *Shurabia ferganensis* Rasnitsyn	[82]	Rasnitsyn 1982
70.	Geinitziidae: *Fletchitzia picturata* Riek	[78]	Riek 1976b
71.	Geinitziidae: *Shurabia australis* Rasnitsyn	[74]	Rasnitsyn 1982
72.	Geinitziidae: *Shurabia sugutensis* Rasnitsyn	[73]	Rasnitsyn 1982
73.	Geinitziidae: *Shurabia ovata* Rasnitsyn	[71]	Martynov 1937a
74.	Mesorthopteridae: *Mesorthopteron similis* Riek	[78]	Riek 1974
75.	Chaeteessidae	[52]	Rasnitsyn 1988
76.	Chateessidae	[39]	Rasnitsyn 1988
77.	Chateessidae: *Chaetoessa brevialata* Siebel	[19]	Siebel 1862; Crowson *et al.* 1967
78.	Mantodea: "Gottesanbeterinnen"	[17]	Schlee & Glockner 1978
79.	Mantidae	[15]	Wilson 1978a
80.	Mantodea	[11]	Baroni-Urbani & Saunders 1982
81.	Mantidae: *Mantis boettingensis* Zeuner	[7]	Zeuner 1931
82.	Archimylacridae: *Aphthoroblattina shottoni* Laurentiaux	[Bashkir]	Laurentiaux 1953
83.	Spiloblattinidae: *Sysciophlebia pygmaea* Meunier, Mesoblattinidae: *Haberleoblatta remigii* Dohrn, Archimylacridae: *Archimylacris diensti* Guthörl	[94]	Dohrn 1897; Meunier 1904b; Guthörl 1934
84.	Mylacridae: *Metaxyblatta gromotuchensis* Bekker-Migdisova	[97]	Bekker-Migdisova 1961
85.	Archimylacridae: *Phyloblatta uralensis* Martynov	[87]	Martynov 1937b
86.	Poroblattinidae: *Triassoblatta simplex* Riek, Mesoblattinidae: *Samaroblatta parvula* Riek	[78]	Riek 1976
87.	Mesoblattinidae: *Sogdoblatta robusta* Martynov, Archimylacridae: *Kisylblatta unifascia* Martynov	[71]	Martynov 1937a
88.	Mesoblattinidae: *Nannoblattina petulantia* Whalley	[69]	Whalley 1985
89.	Mesoblattinidae: *Ptychoblattina dilatata* Bode	[68]	Bode 1953
90.	Mesoblattinidae: *Rhipidoblattina liagouensis* Hong	[64]	Hong 1983
91.	Mesoblattinidae: *Lithoblatta lithophila* Germar	[61]	Germar 1839; Kuhn 1961

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
92.	Raphidiomimidae: *Raphidiomima chimaera* Vishniakova, Mesoblattinidae: *Karatavoblatta longicauda* Vishniakova	[60]	Vishniakova 1968, 1973
93.	Mesoblattinidae	[57]	Jarzembowski 1984
94.	Mesoblattinidae: *Artitoblatta hispanica* Whalley & Jarzembowski 1985	[56]	Whalley & Jarzembowski 1985
95.	Mesoblattinidae	[54]	Sanz *et al.* 1988
96.	Blattidae: ?*Methana*	[53]	Jell & Duncan 1986
97.	Mesoblattinidae	[52]	Rasnitsyn 1988
98.	Mesoblattinidae	[45]	Schlüter 1978
99.	Blattulidae, Blatellidae, Blattidae	[39]	Rasnitsyn 1988
100.	Blattodea "larvae"	[37]	Zherikin & Sukacheva 1973
101.	Blattidae	[32]	Wilson 1978a
102.	Blattodea	[25]	Saunders *et al.* 1974
103.	Blattidae	[24,23]	Wilson 1978a; Lutz 1987
104.	Polyphagidae: *Polyphaga fossilis* Shelford, Blattidae: *Polyzosteria tricuspidata* Germar & Berendt, Blatellidae: *Blatella yolanda* Shelford, Blaberidae: Perisphaeriinae, Nyctiboridae: ?*Nyctibora succini* Shelford	[19]	Germar & Berendt 1856; Shelford 1910; Keilbach 1982
105.	Blattariae ("Schaben")	[17]	Schlee & Glockner 1978
106.	Blattidae	[15]	Wilson 1978a
107.	Blattodea	[11]	Baroni-Urbani & Saunders 1982
108.	Blattoptera ("Schaben")	[6]	Schumann & Wendt 1989
109.	Hodotermitidae: *Meiatermes bertrani* Lacasa-Ruiz & Martinez-Delclós 1986	[56]	Lacasa-Ruiz & Martinez-Delclós 1986
110.	Hodotermitidae: *Valditermes brenanae* Jarzembowski	[57]	Jarzembowski 1981
111.	Hodotermitidae	[52]	Rasnitsyn 1988
112.	Hodotermitidae: *Cretatermes carpenteri* Emerson	[47]	Emerson 1967
113.	Mastotermitidae	[45]	Schlüter 1978
114.	Isoptera	[37]	Zherikin & Sukacheva 1973
115.	Isoptera	[36]	Grimaldi *et al.* 1989
116.	?Mastotermitidae	[35]	Dmitriev & Zherikin 1988
117.	Mastotermitidae	[32]	Wilson 1978a
118.	Kalotermitidae: *Neotermes grassei* Emerson	[27]	Emerson 1969
119.	Mastotermitidae: *Blattotermes wheeleri* Collins	[25]	Emerson 1965
120.	Isoptera	[24]	Lutz 1987
121.	Mastotermitidae: *Idomastotermes mysticus* Haupt	[22]	Emerson 1965
122.	Kalotermitidae: *Electrotermes giradi* (Giebel), Termopsidae: *Termopsis bremii* (Heer)	[19]	Burnham 1978; Keilbach 1982
123.	Kalotermitidae: *Kalotermes disruptus* (Cockerell), Rhinotermitidae: *Reticulitermes* sp.	[18]	Jarzembowski 1976, 1980
124.	Isoptera ("Termiten")	[17]	Schlee & Glockner 1978
125.	Termitidae, Rhinotermitidae, Hodotermitidae, Termopsidae, Kalotermitidae, Mastotermitidae	[15]	Wilson 1978a
126.	Termopsidae: *Calcaritermes vetus* Emerson, Kalotermitidae: *Coptotermes sucineus* Emerson	[11]	Emerson 1969, 1971; Burnham 1978; Keilbach 1982

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
127.	Mastotermitidae: *Ulmeriella martynovi* Zeuner, Kalotermitidae: *Kalotermes rhenanus* Hagen	[9,8]	Zeuner 1938; Emerson 1969
128.	Isoptera ("Termiten")	[6]	Schumann & Wendt 1989
129.	Mastotermitidae: *Mastotermes minor* Pongracz	[5]	Emerson 1965
130.	Kalotermitidae: Cryptotermes ryshkoffi Pierce, Mastotermitidae: *Mastotermes insignis* (Heer)	[4,3]	Emerson 1965, 1969
131.	Sheimiidae: *Sheima sojanensis* Martynova	[86]	Martynova 1958; Crowson *et al.* 1967
132.	Embiidae: *Electroembia antiqua* Pictet	[19]	Pictet 1854; Keilbach 1982
133.	Termopsidae: *Coptotermes priscus* Emerson	[17]	Emerson 1971; Keilbach 1982
134.	Embiidae	[15]	Wilson 1978a
135.	Embioptera	[11]	Baroni-Urbani and Saunders 1982
136.	Chresmodidae: *Prochresmoda longipoda* Sharov	[82]	Sharov 1971(1968)
137.	Aeroplanidae: *Aeroplana mirabilis* Tillyard	[74]	Tillyard 1918; Sharov 1971(1968)
138.	Aerophasmatidae: *Durnovaria parallela* Whalley	[69]	Whalley 1985
139.	Chresmodidae: *Chresmodella integra* Bode	[68]	Bode 1953
140.	Chresmodidae: *Chresmoda obscura* Germar	[61	Germar 1839
141.	Necrophasmatidae: *Necrophasma shabarovi* Martynov, Aerophasmatidae: *Aerophasma prynadai* Martynov	[60]	Martynov 1925, 1928
142.	Prochresmodidae	[52]	Rasnitsyn 1988
143.	Cretophasmatidae	[39]	Rasnitsyn 1988
144.	Phasmatodea	[24]	Lutz 1987
145.	Phasmatidae: *Pseudoperla lineata* Pictet	[19]	Pictet-Baraban & Hagen 1856; Keilbach 1982
146.	Phasmatidae	[15]	Wilson 1978a
147.	Protodiplatidae: *Brevicula gradus* Whalley	[69]	Whalley 1985
148.	Protodiplatidae: *Protodiplatys fortis* Martynov, Pygidicranidae: *SEmenoviola obliquotruncata* Martynov	[60]	Martynov 1925; Crowson *et al.* 1967
149.	?Dermaptera	[33]	George 1952
150.	Forficulidae: *Forficula baltica* Burr, Labiduridae: *?Labidura* sp.	[19]	Burr 1911; Keilbach 1982
151.	Dermaptera ("Ohrwdrmer)	[17]	Schlee & Glockner 1978
152.	Forficulidae	[15]	Wilson 1978a
153.	Dermaptera	[11]	Baroni-Urbani & Saunders 1982
154.	Forficulidae	[6]	Schumann & Wendt 1989
155.	Zorotypidae: *Zorotypus palaeus* Poinar	[17]	Poinar 1988
156.	Dichentomiidae: *Dichentomum tinctum* Tillyard	[90]	Tillyard 1926c; Carpenter 1932
157.	Hoplopleuridae: *Neohaematopinus relictus* Dubinin	[Pleist.]	Laurentiaux 1953
158.	Lophioneuridae: *Tschekardus hispidus* Vishniakova	[89]	Vishniakova 1981
159.	Protoposobolidae: *Protoprosobole straeleni* Laurentiaux	[101]	Laurentiaux 1952
160.	Permaleurodidae: *Permaleurodes rotundatus* Bekker-Migdisova, Permaphidopseidae: *Kaltanaphis permiensis* Bekker-Migdisova, Archescytinidae: *Permopsylla kuznetskiensis* Bekker-Migdisova, Blattoprosobolidae: *Blattoprosobole tomiensis* Bekker-Migdisova 1961, Pereboriidae: *Neuropibrocha ramisubcostalis* Bekker-Migdisova	[97]	Bekker-Migdisova 1961

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
161.	Hydrocorisae	[76]	Olsen *et al.* 1978
162.	Asiocoleidae: *Asiocoleus novojilovi* Rohdendorf, Cupedidae: *Eocupes lujanovitschi* Rohdendorf, Kaltanocoleidae: *Kaltanocoleus pospelovi* Rohdendorf, Permosynidae: *Ademosyne sibirica* Rohdendorf, Taldycupedidae: *Schizotaldicupes ananjevi* Rohdendorf	[97]	Rohdendorf 1961
163.	Family undetermined: *Curculiopsis ellipticus* Martynov	[87]	Martynov 1937b
164.	Cupedidae: *Mesocupoides indistinctus* Ponomarenko, Catiniidae: *Catinoides rotundatus* Ponomarenko, Triaplidae: *Triaplus laticoxa* Ponomarenko	[82]	Ponomarenko 1969a, 1977
165.	?Silphidae: *Pseudosilphites triassicus* Zeuner, Permosynidae: *Ademosyne prisca* Riek, Ommatidae, Cupedidae: *Notemocupes townrowi Zeuner*	[78]	Zeuner 1931, 1961; Riek 1974
166.	*?Nitulidae, ?Buprestidae*	*[76]*	*Olsen et al. 1978*
167.	Scarabaeidae: *Apohrodiites protogaea* Heer; ?Elateridae: *Megacentrus tristis* Heer	[72]	Heer 1865; Crowson 1981
168.	Ommatidae: *Notocupes crassus* Ponomarenko; Coptoclavidae	[71]	Ponomarenko 1969a, 1977
169.	Elateridae: *Elaterina liassica* Gardiner, Cupedidae: *Liassocupes parvus* Zeuner, Drypoidea, ?Carabidae: *Notokistus brodiei* Handlirsch, Byrrhoidea	[69]	Handlirsch 1908; Gardiner 1961; Zeuner 1962; Whalley 1985
170.	Liadytidae: *Angaragabus jurassicus* Ponomarenko	[67]	Ponomarenko 1963; Crowson *et al.*
171.	Coptoclavidae: *Stygeonectes jurassicus* Ponomarenko, Silphidae: *Mesagyrtes communis* Ponomarenko, Hydraenidae: "*Ochtebiites*" *altus* Ponomarenko, Staphylinoidea	[66]	1967; Ponomarenko 1977
172.	Triaplidae, Trachypacheidae, Cupedidae, Cupedidae, Taldycupidae, Nitidulidae, Cerambycidae	[64]	Hong 1983
173.	?Hydrophilidae: *Pseudohydrophilus avitus* Heyden, ?Dryopidae: *Parasilphites angusticollis* Oppenheimer, Scarabaeidae *Geotrupes lithographicus* Deichmüller	[61]	Deichmüller 1886; Ponomarenko 1977; Crowson et al. 1967
174.	Mordellidae: *Praemordella martynovi* Scegoleva-Dascillidae: *Mesodascilla jacobsoni* Martynov; Hydraenidae: "*Ochtebiites*" *altus* Ponomarenko; Cupedidae; Ademosynidae; Catiinide; Schizophoridae; Gyrinidae; Coptoclavidae; Trachypacheidae; Carabidae; Eucinetidae; Byrrhidae; Elateridae; Buprestidae; Scarabaeidae; Staphylinidae; Hydrophilidae; Lophocateridae; Peltidae; Trogossitidae; Protocucujidae; Cucujidae; Scraptiidae; Alleculidae; Chrysomelidae	[60]	Scegoleva-Barovskaya 1929; Crowson et al. 1967; Ponomarenko 1977
175.	Buprestidae: ?*Chrysobotris ballae* Whalley & Jarzembowski	[56]	Whalley & Jarzembowski 1985; Lacasa-Ruiz & Martinez-Delclós 1986
176.	Cupedidae; Elateriformia	[57]	Jarzembowski 1984

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
177.	Cupedidae, Ademosynidae	[54]	Sanz *et al.* 1988
178.	Hydraenidae, Hydrophilidae, Staphylinidae, Pselaphidae, Helodidae, Cantharidae, Mordellidae	[53]	Jell & Duncan 1986
179.	Carabidae, Trachypacheidae, Gyrinidae, Carabidae, Hydrophilidae, Scarabaeidae	[52]	Nitrikin 1977
180.	Trachypacheidae; Staphylinidae: *Stenus inexpectatus* Schlüter	[46,45]	Ponomarenko 1977; Schlüter 1978
181.	Carabidae, Staphylinidae, Scarabaeidae, Elateroidea	[43]	McKay & Rayner 1986
182.	Dytiscidae	[39]	Ponomarenko 1977
183.	Staphylinidae, Cerophytidae, Helodidae, Lathrididae, Passandridae, Cryptophagidae, Throscidae, Acanthocnemidae, Colydiidae	[37]	Zherikin & Sukacheva 1973; Arnoldi et al. 1977
184.	Staphylinidae, Scydmaenidae, Cerambycoidea	[35]	McAlpine & Martin 1969
185.	?Carabidae	[33]	George 1952
186.	Carabidae, Hydrophilidae, ?Noteridae, ?Helodidae, Elateridae, Scarabaeidae, Buprestidae, Chrysomelidae, Tenebrionidae	[32]	Wilson 1978a; Mitchell & Wighton 1979
187.	Carabidae, Scarabaeidae, Eucnemidae, Throscidae, Anobiidae; Coleoptera	[26,25]	Britton 1960; Saunders *et al.* 1974
188.	Carabidae, Staphylinidae, Dascillidae, Lucanidae, Scarabaeidae, Elateridae, Buprestidae, Chrysomelidae, Cerambycidae	[24]	Lutz 1987
189.	Carabidae, Dytiscidae, Hydrophilidae, Staphylinidae, Scarabaeidae, Nosodendridae, Elateridae, Anobiidae, Ptinidae, Nitudulidae, Cucujidae, Cryptophagidae, Erotylidae, Melandryidae, Mordellidae, Rhipiphoridae, Cerambycidae, Bruchidae, Chrysomelidae; Cupedidae, Staphylinoidea, Silphidae, Scarabaeidae, Buprestidae, Elateridae, Oedemeridae, Tenebrionidae, Cerambycidae, Chrysomelidae	[23,22]	Wilson 1978a; Haupt 1950
190.	Cupedidae, Carabidae, Dytiscidae, Gyrinidae, Ptiliidae, Silphidae, Scydmaenidae, Staphylinidae, Pselaphidae, Micromalthidae, Lycidae, Canthariidae, Cleridae, Dascillidae, Helodidae, Circaeidae, Elateridae, Artematopidae, Eucnemidae, Throscidae, Buprestidae, Dryopidae, Dermestidae, Rhizophagidae, Nitudilidae, Cucujidae, Colydiidae, Lathriidae, Mycetophagidae, Anobiidae, Phytidae, Endomychidae, Pedilidae, Pyrochroidae, Aderidae, Scraptiidae, Anthicidae, Meloidae, Rhipiphoridae, Mordellidae, Lagriidae, Alleculidae, Serropalpidae, Tenebrionidae, Cerambycidae, Chrysomelidae, Scarabaeidae, Lucanidae, Curculionidae	[19]	Voss 1953; Larsson 1978; Crowson 1981; Keilbach 1982
191.	Carabidae, Staphylinidae, Elateridae, Endomychidae, Chrysomelidae, Cerambycidae	[17]	Schlee & Glockner 1978

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
192.	Carabidae, Dytiscidae, Hydrophilidae, Silphidae, Staphylinidae, Lucanidae, Scarabaeidae, Helodidae, Dascillidae, Byrrhidae, Psephenidae, Dryopidae, Chelonariidae, Buprestidae, Elateridae, Throscidae, Eucnemidae, Lampyridae, Cantharidae, Lycidae, Melridae, Dermestidae, Anobiidae, Ptinidae, Bostrychidae, Trogossitidae, Cleridae, Cucujidae, Lymexylidae, Nitidulidae, Cryptophagidae, Coccinellidae, Erotylidae, Lathridiidae, Colydiidae, Mycetophagidae, Tenebrionidae, Alleculidae, Pythidae, Melandryidae, Mordellidae, Oedemeridae, Rhipiphoridae, Meloidae, Anthicidae, Bruchidae, Cerambycidae, Chrysomelidae, Anthribidae; Chrysomelidae, Curculionoidea	[15]	Wilson 1978a; Théobald 1937; Crowson 1981
193.	Carabidae, Hydraenidae, Hydrophilidae, Leiodidae, Pselaphidae, Ptiliidae, Scymaenidae, Staphylinidae, Clambidae, Helodidae, Eucinetidae, Artematopidae, Elateridae, Eucnemidae, Throscidae, Byhrrhidae, Anobiidae, Ptinidae, Cleridae, Melyridae, Ostomidae, Dermestidae, Lymexilidae, Sphindidae, Cucujidae, Nitulidae, Phalacridae, Endomychidae, Coccinellidae, Lathriidae, Anthicidae, Colydidae, Cisidae, Mordellidae, Scraptiidae, Oedomeridae, Mycetophagidae, Chrysomelidae, Cerambycidae	[6]	Barthel & Hetzer 1982; Schumann & Wendt 1989
194.	Staphylinidae: *Carpelimus* sp., Nitidulidae: *Cybocephalus* cf. *californicus* Horn	[4]	Palmer 1957
195.	Carabidae, Hydrophilidae, Georyssidae, Ptiliidae, Staphylinidae, Scydmaenidae, Byrrhidae, Anobiidae, Lathridiidae, Colydidae, Chrysomelidae	[1]	Hopkins *et al.* 1971
196.	Myrmecolaccidae: *Stichotrema eocaenicum* (Haupt)	[22]	Haupt 1950; Kinzelbach & Lutz 1985
197.	Permithonidae: *Permithonopsis kaltanensis* Martynova, Palaemerobiidae: *Palaemerobius latibasis* Martynova	[97]	Martynova 1961
198.	Sialidopsidae: *Sialidopsis similis* Martynov	[87]	Martynov 1937b
199.	Permithonidae: *Permithone belmontensis* Tillyard	[83]	Tillyard 1926d
200.	Polystoechidae: *Lithosmylidia lineata* Riek	[79]	Lambkin 1988
201.	Neuroptera	[76]	Olsen *et al. 1978.*
202.	*Palaeomerobiidae: Propsychopsis venosa* Tillyard	[74]	Tillyard 1917
203.	Osmylidae: *Soguta speciosa* Martynova	[73]	Martynova 1958
204.	Mesopolystoechidae: *Mesopolystoechus apicalis*	[71]	Martynov 1937a
205.	Brongniartellidae: *Actinophlebia intermixta* (Scudder), Mesopolystoechidae: *Mesopolystoechus magnificus* Tillyard; Kalligrammitidae: *Paractinophlebia curtsii* (Scudder); Permithonidae: *Archaeosmylus complexus* Whalley	[69]	Whalley 1988
206.	Prohemerobiidae: *Mesosmylina exornata* Bode; Psychopsidae: *Liassopsychops curvata* Bode	[68]	Bode 1953
207.	Mesithonidae: *Sibithone dichotoma* Ponomarenko	[66]	Ponomarenko 1985

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
208.	Osmylitidae: *Sinosmylites pectinatus* Hong, Psychopsidae: *Beipiaopsychops triangulata* Hong, Mesopolystoechidae: *Mesopolystoechus wangyingziensis* Hong	[64]	Hong 1983
209.	Nymphitidae: *Nymphites priscus* (Weyenbergh), Osmylitidae: *Osmylites protogaeus* (Hagen), Mesochrysopidae: *Mesochrysopa zitteli* (Meunier), Kalligrammatidae: *Kalligramma haeckeli* Walther	[61]	Hagen 1862; Weyenbergh 1869; Meunier 1898; Walther 1904; Kuhn 1961
210.	Mesithonidae, Prohemerobiidae, Osmylopsychopsidae, Kalligrammatidae, Osmylidae, Mesochrysopidae, Nymphitidae, Coniopterygidae	[60]	Rasnitsyn 1988
211.	Brongniartiellidae: *Pterinoblattina penna* Scudder	[59]	Scudder 1885; Whalley 1988
212.	Brongniartiellidae, Kalligrammatidae, Psychopsidae	[57]	Rasnitsyn 1988
213.	Mesithonidae, Prohemerobiidae, Mesochrysopidae, Osmylidae, Nymphitidae	[52]	Rasnitsyn 1988
214.	?Myrmeleontidae: *Palaeoleon ferrogeneticus* Rice; Berothidae: *Retinoberotha stuermeri* Schlüter	[47,45]	Rice 1968; Schlüter 1978
215.	Hemerobiidae, Psychopsidae, Ascalaphidae, Nymphitidae	[39]	Rasnitsyn 1988
216.	Coniopterygidae: *Glaesoconis cretica* Meinander	[37]	Meinander 1975
217.	Osmylidae: *Euporismites balli* Tillyard	[30]	Lambkin 1987
218.	Coniopterygidae: *Hemisemidalis sharovi* Meinander, Hemerobiidae: *Prophlebonema resinata* Krüger, Nymphidae: *Pronymphes mengeanus* (Hagen), Ascalaphidae: *Neadelphus protae* MacLeod, Berothidae: *Proberotha prisca* Krüger, Osmylidae: *Protosmylus pictus* (Hagen), Psychopsidae: *Liassopsychops curvata* Bode, Sisyridae: *Sisyra amissa* Hagen	[19]	Pictet-Baraban & Hagen 1856; Krüger 1923; Bode 1953; MacLeod 1970; Meinander 1975; Larsson 1978; Keilbach 1982
219.	Mantispidae: *Promantispa relicta* (Cockerell),	[18]	Jarzembowski 1980
220.	Hemerobiidae: *Hemerobius tinctus* Jarzembowski, Chrysopidae, Sisyridae		
221.	Nemopteridae, Chrysopidae, Hemerobiidae	[15]	Wilson 1978a
222.	Sisyridae: *Sisyra* sp.	[6]	Schumann & Wendt 1989
223.	Mesoraphiididae: *Metaraphidia confusa* Whalley Baissopteridae: *Priscaenigma obtusa* Whalley	[69]	Whalley 1985
224.	Mesoraphidiidae	[60]	Rasnitsyn 1988
225.	Mesoraphidiidae	[57]	Jarzembowski 1984
226.	Mesoraphidiidae	[54]	Sanz *et al.* 1988
227.	Alloraphidiidae	[47]	Carpenter 1967
228.	Inocelliidae	[39]	Rasnitsyn 1988
229.	Raphiidae	[32]	Wilson 1978a
230.	Inocellidae: *Inocellia peculiaris* Carpenter, Raphidiidae: *Raphidia baltica* Carpenter	[19]	Carpenter 1956
231.	Raphidiidae, Inocellidae	[15]	Wilson 1978a
232.	Permosialididae: *Permosialis sibirica* Martynova	[97]	Martynova 1961; Crowson *et al.* 1967
233.	Permosialididae: *Permosialis bifasciata* Martynov	[86]	Sharov 1953; Hennig 1981
234.	Euchauliodidae: *Euchauliodes distinctus* Riek	[78]	Riek 1974

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
235.	Dorniellidae: *Dorniella pulchra* Bode	[68]	Bode 1953
236.	Corydalidae: *Cretochaulius lacustris* Ponomarenko	[52]	Ponomarenko 1976
237.	Corydalidae: *Chauliosialis sukatshevae* Ponomarenko	[37]	Ponomarenko 1976
238.	Sialidae: *Sialis* sp., Corydalidae: *Chauliodes prisca* Pictet	[19]	Pictet-Baraban & Hagen 1856; Keilbach 1982
239.	Sialidae	[15]	Wilson 1978a
240.	Xyelidae: *Xyelimus majus* Rasnitsyn	[82]	Rasnitsyn 1969
241.	Xyelidae: *Archexyela crosbyi* Riek	[79]	Rasnitsyn 1969
242.	Myrmiciidae: *Shurabisca liassica* Rasnitsyn	[71]	Rasnitsyn 1968
243.	Xyelidae: *Liadoxyela praecox* Rasnitsyn	[67]	Rasnitsyn 1966, 1969
244.	Anaxyelidae: *Nygmatius beipiaoensis* Hong, Beipiaosiricidae: *Beipiaosirex parva* Hong, Cephidae: *Sinocephus beipiaoensis* Hong, Sinoryssidae: *Sinoryssus suni* Hong, Pamphiliidae: *Mesolyda rara* Hong	[64]	Hong 1983
245.	Siricidae: *Pseudosirex gracilis* Oppenheim	[61]	Kuhn 1961
246.	Paroryssidae: *Paroryssus extensus* Martynov, Xyelidae: *Microxyelecia brachycera* Rasnitsyn, Xyelotomidae: *Xyelotoma nigricornis* Rasnitsyn, Syntexidae: *Brachysyntexis brachyura* Rasnitsyn, Karatavitidae: *Karatavites jurassicus* Rasnitsyn, Paraoryssidae: *Paroryssus extensus* Martynov, Cephidae: *Mesocephus sibiricus* Rasnitsyn, Siricidae: *Praesirix hirtus* Rasnitsyn	[60]	Martynov 1925; Rasnitsyn 1963, 1968, 1969
247.	Ephialtitidae: *Ephialtites jurassicus* Meunier	[56]	Meunier 1903; Lacasa-Ruiz & Martinez-Delclós 1986
248.	Eoichneumonidae: *Eoichneumon duncanae* Jell & Duncan	[53]	Jell & Duncan 1986
249.	Xyelidae: *Baissoxyela tarsalis* Rasnitsyn, Cephidae: *Mesocephus sibiricus* Rasnitsyn, Siricidae: *Praesirex hirtus* Rasnitsyn	[52]	Rasnitsyn 1968, 1969
250.	Braconidae	[37]	Zherikin & Sukacheva 1973
251.	Braconidae: *Diospilus allani* Brues	[35]	Brues 1937
252.	Ichneumonidae, Braconidae	[23]	Wilson 1978a
253.	Cephidae: *Electrocephus stralendorffi* Konow, Ichneumonidae: *Pimpla succini* Giebel, Braconidae: *Iaeorhyssalus dubitosus* Brues, Electrotomidae: *Electrotoma succini* Rasnitsyn, Siricidae: *Urocerus klebsi* Brues	[19]	Giebel 1856, Brues 1926, 1933; Konow 1897; Rasnitsyn 1977
254.	Ichneumonoidea	[17]	Schlee & Glockner 1978
255.	Orussidae, Siricidae, Tenthredinidae, Braconidae, Pamphilidae, Blasticotomidae, Xyelidae, Cephidae, Ichneumonidae, Stephanidae	[15]	Wilson 1978a
256.	Protomeropeidae: *Altajopanorpa brevis* Martynova	[97]	Martynova 1961
257.	Unnamed family: *Tarwinia australis* Jell & Duncan	[53]	Riek 1970, Jell & Duncan 1986
258.	Tipulidae, Bibionidae	[76]	Olsen *et al.* 1978
259.	Philopotamidae: *Prephilopotamus asiaticus* Sukacheva	[82]	Sukacheva 1973

(ADULT ECTOGNATHATE, continued)

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
260.	Archaeolepidae: *Archaeolepis mane* Whalley	[69]	Whalley 1985, 1986
261.	Eolepidopterygidae: *Eolepidopteryx jurassica*	[62]	Rasnitsyn 1983, Whalley 1986
262.	Eolepidopterygidae	[60]	Rasnitsyn 1988
263.	Micropterygidae: *Parasabatinca aftimacrai* Whalley	[55]	Whalley 1978
264.	Micropterygidae: Undopteryx sukatshevae Skalski	[52]	Skalski 1979a
265.	Micropterygidae	[45]	Schlüter 1978
266.	Micropterygidae: *Micropteryx proavitella* Rebel	[19]	Rebel 1936, Crowson *et al.* 1867
267.	Micropterygidae: *Micropteryx angelica* Jarzem-	[18]	Jarzembowski 1980
268.	Micropterygidae: *Micropteryx* sp.	[5]	Barthel & Hetzer 1982

MOUTHPART CLASS 4: LARVAL ECTOGNATHATE

Fig. 4

1.	Permosialidae: *Permosialis sibirica* Martynova	[97]	Martynova 1961; Crowson et *al.* 1967
2.	Tschekardocoleidae	[92]	Kukalová1969
3.	Asiocoleidae, Cupedidae, Taldycupedidae, Kaltanocoleidae, Permosynidae	[97]	Rohdendorf 1961
4.	Tschekardocoleidae	[89]	Rohdendorf & Ponomarenko 1962; Crowson et *al.* 1967
5.	Cupedidae	[82]	Ponomarenko 1969a; 1977
6.	Ommatidae, Cupedidae, Permosynidae	[78]	Zeuner 1961; Riek 1974
7.	Ommatidae	[73]	Ponomarenko 1969a
8.	Ommatidae	[71]	Ponomarenko 1969a
9.	Cupedidae	[69]	Zeuner 1962
10.	Taldycupidae	[64]	Hong 1983
11.	Cupedidae	[61]	Ponomarenko 1971
12.	Cupedidae, Ademosynidae	[60]	Rohdendorf 1968a
13.	Cupedidae	[57]	Jarzembowski 1984
14.	Cupedidae	[54]	Sanz et *al.* 1988
15.	Ademosynidae, Cupedidae	[52]	Rasnitsyn 1988
16.	Labrodorocoleidae	[47]	Ponomarenko 1969b
17.	Cupedidae	[39]	Rasnitsyn 1988
18.	Cupedidae	[22]	Haupt 1950
19.	Micromalthidae, Cupedidae	[19]	Larsson 1978; Keilbach 1982
20.	Triaplidae	[82]	Ponomarenko 1977b
21.	Coptoclavidae	[71]	Ponomarenko 1969a
22.	Carabidae	[69]	Whalley 1985
23.	?Noteridae	[67]	Ponomarenko 1963
24.	Coptoclavidae	[66]	Ponomarenko 1977b
25.	Caraboidea	[64]	Hong 1983
26.	Parahydrobiidae	[62]	Ponomarenko 1977b
27.	Carabidae	[61]	Kuhn 1961
28.	Schizophoridae, Cyrinidae, Coptoclavidae, Trachypacheidae	[60]	Rasnitsyn 1988
29.	Gyrinidae, Coptoclavidae, Trachypacheidae, Carabidae	[52]	Rasnitsyn 1988

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
30.	Trachypacheidae	[46]	Ponomarenko 1977b
31.	Gyrinidae, Dytiscidae, Carabidae	[39]	Rasnitsyn 1988
32.	?Carabidae	[33]	George 1952
33.	?Noteridae	[32]	Wilson 1978a; Mitchell & Wighton 1979
34.	Carabidae	[26]	Britton 1960
35.	Dytiscidae, Carabidae	[24,23]	Wilson 1978a; Lutz 1987
36.	Gyrinidae, Dytiscidae, Carabidae	[19]	Keilbach 1982
37.	Carabidae	[17]	Schlee & Glockner 1978
38.	Carabidae, Dytiscidae	[15]	Wilson 1978a
39.	Paussidae, Carabidae	[6]	Schumann & Wendt 1989
40.	Carabidae	[1]	Hopkins *et al.* 1971
41.	Catiniidae	[82]	Ponomarenko 1969a
42.	Catiniidae	[52]	Rasnitsyn 1988
43.	Hydraenidae	[66]	Ponomarenko 1977b
44.	?Hydrophilidae	[61]	Crowson *et al.* 1967
45.	Hydraenidae, Hydrophilidae	[60]	Rasnitsyn 1988
46.	Hydrophilidlae, Hydraenidae	[53]	Jell & Duncan 1986
47.	Hydrophilidae	[52]	Rasnitsyn 1988
48.	Hydrophilidae	[39]	Rasnitsyn 1988
49.	Hydrophilidae	[32]	Wilson 1978a; Mitchell & Wighton 1979
50.	Hydrophilidae	[23]	Wilson 1978a
51.	Hydrophilidae	[15]	Wilson 1978a
52.	Hydraenidae, Hydrophilidae	[6]	Schumann & Wendt 1989
53.	Georyssidae, Hydrophilidae	[1]	Hopkins et *al.* 1971
54.	?Silphidae	[78]	Zeuner 1931; Riek 1974
55.	Silphidae	[66]	Ponomarenko 1977b
56.	Staphylinidae	[60]	Rasnitsyn 1988
57.	Pselaphidae, Staphylinidae	[53]	Jell & Duncan 1986
58.	Scydmaenidae, Siphidae, Staphylinidae	[52]	Rasnitsyn 1988
59.	Staphylinidae	[45]	Schlüter 1978
60.	Staphylinidae	[37]	Zherikin & Sukacheva 1973
61.	Scydmaenidae, Staphylinidae	[35]	McAlpine & Martin 1969
62.	Staphylinidae	[24,23]	Wilson 1978a, Lutz 1987
63.	Silphidae, Staphylinidae	[22]	Wilson 1978a
64.	Ptiliidae, Silphidae, Scydmaenidae, Pselaphidae, Staphylinidae	[19]	Larsson 1978; Keilbach 1982
65.	Staphylinidae	[17]	Schlee & Gloeckner 1978
66.	Silphidae, Staphylinidae	[15]	Wilson 1978a
67.	Leiodidae, Pselaphidae, Ptiliidae, Scymaenidae, Staphylinidae	[6]	Schumann & Wendt 1989
68.	Staphylinidae	[4]	Palmer 1957
69.	Ptiliidae, Scydmaenidae, Staphylinidae	[1]	Hopkins *et al.* 1971
70.	Ademosynidae	[Trias]	Ponomarenko 1977b; Crowson 1981
71.	Eucinetidae, Ademosynidae	[60]	Crowson *et al.* 1967; Rasnitsyn 1988
72.	Helodidae	[53]	Jell & Duncan 1986
73.	Scirtidae, Eucinetidae	[52]	Rasnitsyn 1988

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
74.	Helodidae	[37]	Zherikin & Sukacheva 1973
75.	?Helodidae	[32]	Wilson 1978a; Mitchell & Wighton 1979
76.	Helodidae	[19]	Keilbach 1982
77.	Helodidae	[15]	Wilson 1978a
78.	Clambidae, Eucinetidae, Helodidae	[6]	Schumann & Wendt 1989
79.	Dascillidae	[60]	Ponomarenko 1977b
80.	Dascillidae	[24]	Lutz 1987
81.	Dascillidae	[19]	Keilbach 1982
82.	Dascillidae	[15]	Wilson 1978a
83.	Scarabaeidae	[72]	Crowson 1981
84.	Scarabaeidae	[61]	Ponomarenko 1977b
85.	Scarabaeidae	[60]	Rasnitsyn 1988
86.	Scarabaeidae	[52]	Rasnitsyn 1988
87.	Passalidae, Scarabaeidae	[39]	Rasnitsyn 1988
88.	Scarabaeidae	[32]	Wilson 1978a
89.	Scarabaeidae	[26]	Britton 1960
90.	Lucanidae, Scarabaeidae	[24,23]	Wilson 1978a; Lutz 1987
91.	Scarabaeidae	[22]	Haupt 1950
92.	Lucanidae, Scarabaeidae	[19]	Keilbach 1982
93.	Lucanidae, Scarabaeidae	[15]	Wilson 1978a
94.	Byrrhoidea	[69]	Whalley 1985
95.	Byrrhidae	[60]	Rasnitsyn 1988
96.	Byrrhidae	[52]	Rasnitsyn 1988
97.	Byrrhidae	[15]	Wilshon 1978a
98.	Byrrhidae	[6]	Schumann & Wendt 1989
99.	Byrrhidae	[1]	Hopkins *et al.* 1971
100.	Dryopoidea	[69]	Whalley 1985
101.	?Dryopidae	[61]	Ponomarenko 1971
102.	Dryopidae	[19]	Keilbach 1982
103.	Chelonariidae, Psephenidae, Dryopidae	[15]	Wilson 1978a
104.	?Buprestidae	[76]	Olsen *et al.* 1978
105.	Buprestidae	[61]	Ponomarenko 1971
106.	Buprestidae	[60]	Rasnitsyn 1988
107.	Buprestidae	[56]	Whalley & Jarzembowski 1985
108.	Buprestidae	[52]	Rasnitsyn 1988
109.	Buprestidae	[39]	Rasnitsyn 1988
110.	Buprestidae	[32]	Wilson 1978a; Mitchell And Wighton 1979
111.	Buprestidae	[24]	Lutz 1987
112.	Buprestidae	[19]	Larsson 1978; Keilbach 1982
113.	Buprestidae	[15]	Wilson 1987a
114.	?Elateridae	[72]	Heer 1865
115.	Elateridae	[69]	Whalley 1985
116.	Elateridae	[60]	Rasnitsyn 1988
117.	Cerophytidae, Throscidae, Elateridae	[52]	Rasnitsyn 1988
118.	Elateridae	[39]	Rasnitsyn 1988
119.	Throscidae, Cerphytidae	[37]	Zherikin & Sukacheva 1973
120.	Elateridae	[32]	Wilson 1978a; Mitchell & Wighton 1979

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
121.	Throscidae	[26]	Britton 1960
122.	Elateridae	[24,23]	Wilson 1978a; Lutz 1987
123.	Elateridae	[22]	Haupt 1950
124.	Artematopidae, Eucnemidae, Elateridae, Throscidae	[19]	Larsson 1978; Keilbach 1982
125.	Elateridae	[17]	Schlee & Glockner 1978
126.	Eucnemidae, Throscidae, Elateridae	[15]	Wilson 1978a
127.	Eucnemidae, Elateridae, Throscidae	[6]	Schumann & Wendt 1989
128.	Cantharidae	[53]	Jell & Duncan 1986
129.	Anobiidae	[52]	Rasnitsyn 1988
130.	Anobiidae	[26]	Britton 1960
131.	Anobiidae	[23]	Wilson 1978a
132.	Anobiidae	[19]	Larsson 1978; Keilbach 1982
133.	Bostrychidae, Anobiidae	[15]	Wilson 1978a
134.	Anobiidae	[6]	Schumann & Wendt 1989
135.	Anobiidae	[1]	Hopkins et al. 1971
136.	Nosodendridae	[23]	Wilson 1978a
137.	Dermestidae	[19]	Larsson 1978, Keilbach 1982
138.	Dermestidae	[15]	Wilson 1978a
139.	Dermestidae	[6]	Schumann & Wendt 1989
140.	Lophocateridae, Peltidae, Trogossitidae	[60]	Rasnitsyn 1988
141.	Trogossitidae	[52]	Rasnitsyn 1988
142.	Peltidae, Melyridae	[39]	Rasnitsyn 1988
143.	Acanthocnemidae	[37]	Zherikin & Sukacheva 1973
144.	Cleridae	[19]	Larsson 1978; Keilbach 1982
145.	Melyridae, Trogossitidae	[15]	Wilson 1978a
146.	Ostomidae, Cleridae, Melyridae	[6]	Schumann & Wendt 1989
147.	Lymexylidae	[15]	Wilson 1978a
148.	Lymexylidae	[6]	Schumann & Wendt 1989
149.	?Nitidulidae	[76]	Olsen et al. 1978
150.	Nitidulidae	[64]	Hong 1983
151.	Protocucujidae, Cucujidae	[60]	Rasnitsyn 1988
152.	Coccinellidae	[52]	Rasnitsyn 1988
153.	Cucujidae	[39]	Rasnitsyn 1988
154.	Passandridae, Lathridiidae	[37]	Zherikin & Sukacheva 1973
155.	Cryptophagidae, Erotylidae, Cucujidae, Nitidulidae	[23]	Wilson 1978a
156.	Lathridiidae, Rhizophagidae, Nitidulidae,	[19]	Larsson 1978; Keilbach 1982
157.	Endomychidae	[17]	Schlee & Glockner 1978
158.	Erotylidae, Coccinellidae, Lathridiidae, Cryptophagidae, Cucujidae, Nitidulidae	[15]	Wilson 1978a
159.	Sphindidae, Coccinellidae, Cucujidae, Lathriidae, Endomychidae, Nitidulidae, Phalacridae	[6]	Schumann & Wendt 1989
160.	Nitidulidae	[4]	Palmer 1957
161.	Lathriidae	[1]	Hopkins et al. 1971
162.	Mordellidae, Scraptiidae, Tenebrionidae	[60]	Rasnitsyn 1988
163.	Mordellidae	[53]	Jell and Duncan 1986
164.	Scraptiidae, Colydiidae	[52]	Rasnitsyn 1988
165.	Colydiidae	[37]	Zherikin & Sukacheba 1973

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
166.	Tenebrionidae	[32]	Wilson 1978a
167.	Rhipiphoridae, Mordellidae, Melandridae	[23]	Wilson 1978a, Grande 1980
168.	Oedemeridae, Tenebrionidae	[22]	Haupt 1950
169.	Pyrochroidae, Scraptiidae, Colydiidae, Aderidae, Mycetophagidae, Anthicidae, Meloidae, Lagriidae, Rhipiphoridae, Mordellidae, Tenebrionidae	[19]	Larsson 1978; Keilbach 1982
170.	Pythidae, Colydiidae, Melandryidae, Mordellidae, Mycetophagidae, Tenebrionidae, Rhipiphoridae, Oedomeridae, Meloidae, Anthicidae	[15]	Wilson 1978a
171.	Aderidae, Mordellidae, Scraptiidae, Anthicidae, Mycetophagidae, Cisidae, Colydiidae, Oedomeridae	[6]	Schumann & Wendt 1989
172.	Colydiidae, Lathridiidae	[1]	Hopkins *et al.* 1971
173.	Cerambycidae	[64]	Hong 1983
174.	Chrysomelidae	[60]	Rasnitsyn 1988
175.	Cerambycidae, Chrysomelidae	[52]	Rasnitsyn 1988
176.	Cerambycoidea	[35]	McAlpine & Martin 1969
177.	Chrysomelidae	[32]	Mitchell & Wighton 1979
178.	Bruchidae, Cerambycidae, Chrysomelidae	[23]	Wilson 1978a
179.	Chrysomelidae	[22]	Haupt 1950
180.	Chrysomelidae, Cerambycidae	[19]	Larsson 1978; Keilbach 1982
181.	Cerambycidae, Chrysomelidae	[17]	Schlee & Glockner 1978
182.	Bruchidae, Chrysomelidae, Cerambycidae	[15]	Wilson 1978a
183.	Chrysomelidae	[13]	Théobald 1937
184.	Cerambycidae, Chrysomelidae	[6]	Schumann & Wendt 1989
185.	Chrysomelidae	[1]	Hopkins *et al.* 1971
186.	Curculionidae	[69]	Whalley 1985
187.	Eobelidae	[60]	Arnoldi 1977
188.	Eobelidae, Curculionoidea *incertae sedis*	[56]	Whalley & Jarzembowski 1985
189.	Scolytid tunnels	[57]	Jarzembowski 1984
190.	Attelabidae, Curculionidae	[52]	Zherikin 1977
191.	Curculionidae	[50]	Northrop 1928
192.	Curculionidae	[43]	McKay & Rayner 1986
193.	Curculionidae	[36]	Grimaldi *et al.* 1989
194.	Curculionidae	[32]	Mitchell & Wighton 1979
195.	Curculionidae	[26]	Britton 1960
196.	Anthribidae, Attelabidae, Curculionidae; Curculionoidea	[24,23]	Wilson 1978a; Lutz 1987
197.	Curculionidae	[22]	Haupt 1950
198.	Apionidae, Anthribidae, Curculionidae	[19]	Keilbach 1982
199.	Platypodidae, Curculionidae	[17]	Schlee & Glockner 1978
200.	Anthribidae, Attelabidae, Curculionidae	[15]	Wilson 1978a
201.	Curculionoidea	[13]	Crowson 1981
202.	Platypodidae, Curculionidae	[11]	Keilbach 1982
203.	Apionidae, Curculionidae	[7,6]	Zeuner 1931, Schumann & Wendt 1989
204.	Curculionidae	[1]	Hopkins *et al.* 1971
205.	Megaloptera (Permosialidae): *Permosialis bifasciata* Martynov	[97]	Hennig 1981
206.	Protomeropeidae: *Tomiochorista nubila* Martynova	[97]	Martynova 1958

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
207.	Protomeropeidae: *Platychorista venosa* Tillyard	[90]	Tillyard 1926b
208.	Protomeropeidae: *Marimerobius splendens* Zalessky	[89]	Zalessky 1946
209.	Meropeidae: *Thaumatomerope sogdiana* Rasnitsyn	[82]	Ponomarenko & Rasnitsyn 1974
210.	Meropeidae: *Eomerope asiatica* Ponomarenko	[31]	Ponomarenko & Rasnitsyn 1974
211.	Meropeidae: *Eomerope tortriciformis* Cockerell	[15]	Cockerell 1909d, Ponomarenko & Rasnitsyn 1974
212.	Robinjohniidae: *Robinjohnia tillyardi* Martynova, Nannochoristidae: *Permochorista australica* Tillyard	[83]	Tillyard 1926d; Riek 1970b; Hennig 1981
213.	Nannochoristidae: *Afristella delicatula* Riek	[78]	Riek 1974
214.	Choristidae: *Mesochorista proavita* Tillyard	[74]	Tillyard 1923c
215.	Nannochoristidae: *Mesopanorpa umbrata* Martynov, Orthophlebiidae: *Orthophlebia angustata* Martynov, Neorthophlebiidae: *Neorthophlebia robusta* Martynov	[71]	Martynov 1937a
216.	Orthophlebiidae: *Orthophlebia cappilata* Whalley	[69]	Whalley 1985
217.	Neorthophlebiidae: *Protobittacus arculatus* Bode, Orthophlebiidae: *Protorthophlebia cuneata* Bode	[68]	Bode 1953
218.	Nannochoristidae: *Mesopanorpa luanpingensis* Hong, Orthophlebiidae: *Protorthophlebia yaogouensis* Hong	[64]	Hong 1983
219.	Bittacidae: *Probittacus avitus* Martynov, Orthophlebiidae: *Orthophlebia grandis* Martynov, Panorpidae	[60]	Rohdendorf 1968; Rasnitsyn 1988
220.	Nannochoristidae: *Mesopanorpa* sp., Orthophlebiidae: *Prorthophlebia* sp.	[57]	Jarzembowski 1984
221.	Orthophlebiidae: Orthophlebiinae	[54]	Sanz *et al.* 1988
222.	Choristidae: *Cretacochorista parva* Jell & Duncan, Nannochoristidae: *Prochoristella leongnatha* Jell & Duncan, Orthophlebiidae: *Prorthophlebia* sp.	[53]	Jell & Duncan 1986
223.	Bittacidae, Panorpidae	[52]	Rasnitsyn 1988
224.	Bittacidae	[23]	Grande 1980
225.	Panorpodidae: *Panorpodes brevicauda* Hagen, Panorpidae: *Panorpa obsoleta* Carpenter, Bittacidae: *Bittacus fossilis* Carpenter	[19]	Hagen 1956, Carpenter 1954, Larsson 1978, Keilbach 1982
226.	Bittacidae: *Bittacus veternus* Cockerell	[18]	Jarzembowski 1980
227.	Bittacidae, Panorpidae	[15]	Wilson 1978a
228.	Boreidae	[Malm]	Rasnitsyn 1988
229.	Unnamed family: *Tarwinia australis* Jell & Duncan	[53]	Jell & Duncan 1986
230.	"Pulicid indet."	[53]	Jell & Duncan 1986
231.	Leporid host biogeography	[E. Tert]	Traub & Rothschild 1983
232.	Marsupial host biogeography and fossil record	[L. Cret]	Traub & Rothschild 1983
233.	Hystricopsyllidae: *Palaeopsylla klebsiana* Dampf	[19]	Dampf 1910; Keilbach 1982
234.	Cricetid host biogeography	[E. Tert]	Traub & Rothschild 1983
235.	Chiropteran host fossil record	[E. Tert]	Grande 1980; Traub & Rothschild 1983
236.	Tipulidae, Bibionidae	[76]	Olsen *et al.* 1978
237.	Philopotamidae: *Prephilopotamus asiaticus* Suka-	[82]	Sukacheva 1973
238.	Eolepidopterygidae	[62]	Rasnitsyn 1988
239.	Eolepidopterygidae: *Eolepidopteryx jurassica*	[60]	Rasnitsyn 1983a; Whalley 1986
240.	Eolepidopterygidae: *Daiopteryx rasnitsyni* Skalski	[52]	Skalski 1984b; Whalley 1986

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
207.	Protomeropeidae: *Platychorista venosa* Tillyard	[90]	Tillyard 1926b
208.	Protomeropeidae: *Marimerobius splendens* Zalessky	[89]	Zalessky 1946
209.	Meropeidae: *Thaumatomerope sogdiana* Rasnitsyn	[82]	Ponomarenko & Rasnitsyn 1974
210.	Meropeidae: *Eomerope asiatica* Ponomarenko	[31]	Ponomarenko & Rasnitsyn 1974
211.	Meropeidae: *Eomerope tortriciformis* Cockerell	[15]	Cockerell 1909d, Ponomarenko & Rasnitsyn 1974
212.	Robinjohniidae: *Robinjohnia tillyardi* Martynova, Nannochoristidae: *Permochorista australica* Tillyard	[83]	Tillyard 1926d; Riek 1970b; Hennig 1981
213.	Nannochoristidae: *Afristella delicatula* Riek	[78]	Riek 1974
214.	Choristidae: *Mesochorista proavita* Tillyard	[74]	Tillyard 1923c
215.	Nannochoristidae: *Mesopanorpa umbrata* Martynov, Orthophlebiidae: *Orthophlebia angustata* Martynov, Neorthophlebiidae: *Neorthophlebia robusta* Martynov	[71]	Martynov 1937a
216.	Orthophlebiidae: *Orthophlebia cappilata* Whalley	[69]	Whalley 1985
217.	Neorthophlebiidae: *Protobittacus arculatus* Bode, Orthophlebiidae: *Protorthophlebia cuneata* Bode	[68]	Bode 1953
218.	Nannochoristidae: *Mesopanorpa luanpingensis* Hong, Orthophlebiidae: *Protorthophlebia yaogouensis* Hong	[64]	Hong 1983
219.	Bittacidae: *Probittacus avitus* Martynov, Orthophlebiidae: *Orthophlebia grandis* Martynov, Panorpidae	[60]	Rohdendorf 1968; Rasnitsyn 1988
220.	Nannochoristidae: *Mesopanorpa* sp., Orthophlebiidae: *Prorthophlebia* sp.	[57]	Jarzembowski 1984
221.	Orthophlebiidae: Orthophlebiinae	[54]	Sanz *et al.* 1988
222.	Choristidae: *Cretacochorista parva* Jell & Duncan, Nannochoristidae: *Prochoristella leongnatha* Jell & Duncan, Orthophlebiidae: *Prorthophlebia* sp.	[53]	Jell & Duncan 1986
223.	Bittacidae, Panorpidae	[52]	Rasnitsyn 1988
224.	Bittacidae	[23]	Grande 1980
225.	Panorpodidae: *Panorpodes brevicauda* Hagen, Panorpidae: *Panorpa obsoleta* Carpenter, Bittacidae: *Bittacus fossilis* Carpenter	[19]	Hagen 1856, Carpenter 1954, Larsson 1978, Keilbach 1982
226.	Bittacidae: *Bittacus veternus* Cockerell	[18]	Jarzembowski 1980
227.	Bittacidae, Panorpidae	[15]	Wilson 1978a
228.	Boreidae	[Malm]	Rasnitsyn 1988
229.	Unnamed family: *Tarwinia australis* Jell & Duncan	[53]	Jell & Duncan 1986
230.	"Pulicid indet."	[53]	Jell & Duncan 1986
231.	Leporid host biogeography	[E. Tert]	Traub & Rothschild 1983
232.	Marsupial host biogeography and fossil record	[L. Cret]	Traub & Rothschild 1983
233.	Hystricopsyllidae: *Palaeopsylla klebsiana* Dampf	[19]	Dampf 1910; Keilbach 1982
234.	Cricetid host biogeography	[E. Tert]	Traub & Rothschild 1983
235.	Chiropteran host fossil record	[E. Tert]	Grande 1980; Traub & Rothschild 1983
236.	Tipulidae, Bibionidae	[76]	Olsen *et al.* 1978
237.	Philopotamidae: *Prephilopotamus asiaticus* Suka-	[82]	Sukacheva 1973
238.	Eolepidopterygidae	[62]	Rasnitsyn 1988
239.	Eolepidopterygidae: *Eolepidopteryx jurassica*	[60]	Rasnitsyn 1983a; Whalley 1986
240.	Eolepidopterygidae: *Daiopteryx rasnitsyni* Skalski	[52]	Skalski 1984b; Whalley 1986

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
241.	Archaeolepidae: *Archaeolepis mane* Whalley	[69]	Whalley 1985; 1986
242.	Micropterygidae: *Parasabatinca aftimacrai* Whalley	[55]	Whalley 1978; 1986
243.	Micropterygidae: *Palaeosabatinca zherichini* Kozlov	[52]	Kozlov 1988b
244.	Unnamed micropterygid	[45]	Schlüter 1975, 1978
245.	Micropterygidae: *Sabatinca proavitella* Rebel	[19]	Rebel 1935; Larsson 1978
246.	Micropterygidae: *Micropteryx angelica* Jarzembowski	[18]	Jarzembowski 1980
247.	?Eriocraniidae: *Undopteryx sukatshevi* Skalski	[52]	Skalski 1979a; Whalley 1986
248.	"Lophocoronid-like specimen"	[37]	Skalski 1979b
249.	"Incurvariine type"	[55]	Whalley 1977, Hennig 1981

MOUTHPART CLASS 5: MAXILLOLABIATE

Fig. 43

1.	Megaspilidae: *Allocotidus bruesi* Muesebeck	[40]	Muesebeck 1963
2.	Maimetshidae: *Maimetsha arctica* Rasnitsyn	[37]	Rasnitsyn 1975
3.	Stigmaphronidae: *Lygocerus(?) dubiatus* Brues	[35]	Masner & Dessart 1967
4.	Calliceratidae: *Conostigmus succinalis* Brues	[19]	Brues 1940b
5.	Heloridae: *Protohelorus mesozoicus* Kozlov, Proctotrupidae: *Mesoserphus karatavicus* Kozlov, Monomachidae, Diapriidae	[60]	Martynov 1925, Kozlov 1968
6.	"Proctotrupid indet."	[53]	Jell & Duncan 1986
7.	Pelecinidae: *Iscopinus baissicus* Kozlov	[52]	Kozlov 1974
8.	Scelionidae: *Cenomanioscelio pulcher* Schlüter, Diapriidae: Ismarinae	[45]	Schlüter 1978
9.	Scelionidae, ?Vanhorniidae, Diapriidae, Serphitidae	[37]	Zherikin & Sukacheva 1973
10.	Serphitidae: *Serphites paradoxus* Brues, Scelionidae: *Proteroscelio antennalis* Brues, ?Vanhorniidae	[35]	Brues 1937, McAlpine & Martin 1969
11.	Proctotrupidae: *Cryptoserphus pinorus* Brues, Scelionidae: *Pelecinopteron tubuliforme* Brues, Diapriidae: *Ambositra* sp.	[19]	Brues 1933, 1940a; Masner 1969
12.	Diapriidae: *Galesimorpha wheeleri* Brues, Belytidae: *Belyta mortuella* Brues	[15]	Brues 1910
13.	Scelionidae: *Palaegyron muesbecki* Masner	[11]	Masner 1969
14.	Scelionidae: *Platygasterites femoralis* Statz, Heloridae: *Helorus festivus* Statz 1938	[8]	Statz 1938
15.	Mymaridae: *Galloromma bezonnaisensis* Schlüter	[45]	Schlüter 1978
16.	Eulophidae	[40]	Lagenheim *et al.* 1960
17.	Mymaridae, Chalcidoidea	[37]	Zherikin & Sukacheva 1973; Rasnitsyn 1975
18.	Trichogrammatidae: *Enneagmus pristinus* Yoshimoto, Tetracampidae: *Distylopus bisegmentatus* Yoshimoto, Mymaridae: *Triadomerus bulbosus* Yoshimoto	[35]	Yoshimoto 1975
19.	"Possibly an encyrtid chalcidoid"	[33]	George 1952
20.	Mymaridae	[25]	Saunders *et al.* 1974
21.	Chalcidoidea: *Arescon armata* (Meunier)	[19]	Meunier 1905a

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
58.	Formicidae: *Peltopone petiolata* Dlussky	[39]	Dlussky 1975
59.	Formicidae: *Cretymyrma arnoldi* Dlussky	[37]	Dlussky 1975
60.	Formicidae: *Sphecomyrma freyi* Wilson, Carpenter & Brown	[36]	Wilson, Carpenter & Brown 1967b; Grimaldi *et al.* 1989
61.	Formicidae: ?*Sphecomyrma* sp.	[35]	Burnham 1978
62.	Formicidae	[25]	Saunders *et al.* 1974
63.	Formicidae: Dolichoderinae	[24]	Lutz 1987
64.	Formicidae: *Polanskiella smekali* De Garcia	[20]	De Garcia 1983
65.	Formicidae: *Prionomyrmyx*, sp.	[19]	Burnham 1978; Larsson 1978
66.	Formicidae: *Oecophylla* sp.	[18]	Jarzembowski 1976
67.	Formicidae: *Archimyrmyx rostratus* Cockerell	[15]	Carpenter 1930
68.	Formicidae: Dolichoderinae, aff. *Tapinoma*	[6]	Barthel & Hetzer 1982
69.	Formicidae: *Camponotus* sp.	[1]	Hopkins *et al.* 1971
70.	Sphecidae: *Archisphex crowsoni* Evans	[57]	Evans 1969
71.	Sphecidae: Pemphredonine indet.	[53]	Jell & Duncan 1986
72.	Sphecidae: *Cretosphex incertus* rasnitsyn	[52]	Rasnitsyn 1975
73.	Sphecidae: *Gallosphex cretaceus* Schlüter	[45]	Schlüter 1978
74.	Sphecidae: *Taimyrisphex pristinus* Evans	[37]	Evans 1973
75.	Sphecidae: *Lisponema singularis* Evans	[35]	Evans 1969
76.	Sphecidae: *Crabosuccinalis* sp.	[19]	Cockerell 1909e; Keilbach 1982
77.	Sphecidae	[8]	Bohart & Mencke 1976
78.	Sphecidae: *Passaloecus munax* Sorg	[6]	Sorg 1986
79.	Apidae: *Trigona prisca* Michener & Grimaldi	[36]	Michener & Grimaldi 1989a,b

MOUTHPART CLASS 6: RAPTORIAL ECTOGNATHATE

Fig. 46

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
1.	Protorthoptera (Paoliidae): *Ampeliptera limburgica* Pruvost	[100]	Pruvost 1927; Brauckmann 1988
2.	Bojophlebiidae: *Bojophlebia prokopi* Kukalová-Peck	[98]	Kukalová-Peck 1985
3.	Kennedyidae: *Sushkina parvula* Martynov; Permolestidae: *Epilestes kargalensis* Martynov	[87,86]	Martynov 1930, 1932, 1937a; Crowson
4.	Kennedyidae: *Kennedya gracilis* Pritykina	[82]	Pritykina 1981
5.	Liassogomphidae: *Liassogomphus propinquus* Bode	[69]	Bode 1905; Crowson *et al.* 1967
6.	Permagrionidae: *Permagrion falklandicum* Tillyard	[85]	Tillyard 1928c; Crowson *et al.* 1967
7.	Triassagrionidae: *Triassagrion australiense* Tillyard	[79]	Tillyard 1922; Crowson *et al.* 1967
8.	Protomyrmeleontidae	[68]	Bode 1953
9.	Protomyrmeleontidae: *Protomyrmeleon handlirschii* Martynov	[60]	Martynov 1927b; Crowson *et al.* 1967
10.	Erasipteridae: *Erasipteroides valentini* Brauckmann Meganeuridae: *Namurotypus sippeli* Brauckman & Zessin	[99]	Brauckmann *et al.* 1985; Brauckmann & Zessin 1989
11.	Erasipteridae: *Erasipteron larischi* Pruvost	[98]	Pruvost 1933; Crowson *et al.* *1967*
12.	*Meganeuridae*: *Meganeura monyi* (Brongniart)	[95]	Brongniart 1884; Braucknann & Zessin 1989
13.	Meganeuridae: *Ephemerites rueckerti* Geinitz	[94]	Geinitz 1865; Brauckmann & Zessin 1989

(RAPTORIAL-ECTOGNATHATE, continued)

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
14.	Meganeuridae: *Stephanotypus* sp.	[92]	Brauckmann & Zessin 1989
15.	Meganeuridae: *Meganeuropsis permiana* Carpenter	[90]	Carpenter 1977; Brauckmann & Zessin 1989
16.	Meganeuridae: *Arctotypus sylvaensis* Martynov	[89]	Martynov 1940; Brauckmann & Zessin 1989
17.	Meganeuridae: *Arctotypus sinuatus* Martynov	[86]	Martynov 1931; Brauckmann & Zessin 1989
18.	Triadophlebiidae: *Triadophlebia distincta* Pritykina	[82]	Pritykina 1981
19.	Paralogidae: *Triassologus biseriatus* Riek	[78]	Riek 1976
20.	Meganeuridae: *Liadotypus relictus* Martynov	[71]	Martynov 1937a
21.	Callimokaltaniidae: *Callimokaltania martynovi*	[97]	Zalessky 1955
22.	Ditaxyneuridae: *Ditaxyneura anomalostigma* Tillyard	[89]	Tillyard 1925b; Crowson *et al.* 1967
23.	Polytaxineuridae: *Polytaxineura stanleyi* Tillyard	[83]	Tillyard 1935b; Crowson *et al.* 1967
24.	Gomphitidae	[68]	Bode 1953
25.	Petaluridae: *Mesuropetala costalis* Pritykina, Gomphidae: *Protolindenia deichmuelleri* Pritykina	[60]	Pritykina 1968
26.	Aeschnidae: *Palaeschna pallerolae* Gomez	[56]	Gomez 1979; Lacasa-Ruiz & Martinez-Delclo's 1986
27.	Aeschnidae	[57]	Jarzembowski 1984
28.	Aeschnidae	[54]	Sanz *et al.* 1988
29.	Aeshnidae: *Baissaeshna prisca* Pritykina	[52]	Pritykina 1977
30.	Gomphidae	[32]	Mitchell & Wighton 1979
31.	Gomphidae: *Gomphus resinatus* Pictet	[19]	Pictet-Baraban & Hagen 1856; Larsson 1978
32.	Gomphidae, Aeshnidae	[15]	Wilson 1978a
33.	Aeschnidae: *Projagoria conjuncta* Martynov	[9]	Zeuner 1938
34.	Aeschnidae: *Aeschnidarum* sp.	[7]	Zeuner 1931
35.	Aeschnidiidae	[54]	Sanz *et al.* 1988
36.	Aeschnidiidae: *Leptaeschnidium latum* Pritykina	[52]	Pritykina 1977
37.	Libellulidae	[23]	Wilson 1978a
38.	Libellulidae	[15]	Wilson 1978a
39.	Libellulidae: *Trameobasileus moguntiacus* Zeuner	[9]	Zeuner 1938
40.	Libellulidae: ?*Orthemis* sp.	[4]	Palmer 1957
41.	Triassolestidae: *Triassolestodes asiaticus* Pritykina	[82]	Pritykina 1981
42.	Triassolestidae: *Mesophlebia antinodalis* Tillyard	[79]	Tillyard 1916
43.	Triassolestidae: *Triassologus biseriatus* Riek	[78]	Riek 1976
44.	Triassolestidae: *Triassolestes epiophlebioides*	[74]	Tillyard 1918
45.	Progomophlebiidae	[68]	Bode 1953
46.	Family undetermined: *Triassoneura primitiva* Pritykina	[?82]	Pritykina 1981
47.	?Tarsophlebiidae: *Triassophlebia stigmatica*	[79]	Tillyard 1922
48.	Liassophlebiidae: *Xanthohypsa tillyardi* Pritykina	[73]	Pritykina 1970
49.	Liassophlebiidae: *Hyposothemis fraseri* Whalley	[69]	Whalley 1985
50.	Tarsophlebiidae, Liassophlebiidae, Archithemidae	[68]	Bode 1953
51.	Liassophlebiidae: *Liassophlebia chengdeensis* Hong	[64]	Hong 1983

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
52.	Asiopteridae: *Asiopteron antiquum* Pritykina, Oreopteridae: *Oreopteron asiaticum* Pritykina, Karatawiidae: *Melanohypsa angulata* Pritykina, Euthemistidae: *Euthemis mukltivenosa* Pritykina, Tarsophlebiidae: *Turanophlebia martynovi* Pritykina, Heterophlebiidae: *Erichschmidtia nigrimontana* Pritykina	[60]	Pritykina 1968
53.	Oreopteridae	[Hauter/ Barrem]	Dmitriev & Zherikin 1988
54.	Tarsophlebiidae, Euthemistidae	[57]	Jarzembowski 1984
55.	Karatawiidae: *Macholanda crassicosta* Pritykina, Tarsophlebiidae: *Turanophlebia sibirica* Pritykina	[52]	Pritykina 1977
56.	Steleopteridae: *Auliella crucigera* Pritykina	[60]	Pritykina 1968
57.	Calopterygidae	[23]	Wilson 1978a
58.	Calopterygidae	[15]	Wilson 1978a
59.	Lestidae	[Oligoc]	Dmitriev & Zherikin 1988
60.	Coenagrionidae: *Malmagrion eichstattiense* Hagen	[61]	Hagen 1862
61.	Coenagrionidae	[60]	Rasnitsyn 1988
62.	Coenagrioniidae	[57]	Jarzembowski 1984
63.	Coenagrionid indet.	[53]	Jell & Duncan 1986
64.	Coenagrionidae: *Agrion antiquum* Pictet & Hagen, Platycnemidae: *Platycnemis antiqua* Pictet & Hagen	[19]	Pictet-Baraban & Hagen 1856; Larsson 1978; Keilbach 1982
65.	Platycnemidae, Coenagrionidae	[15]	Wilson 1978a
66.	Stenophlebiidae: *Stenophlebia karatavica* Pritykina	[60]	Pritykina 1968

MOUTHPART CLASS 1: MORTAR-AND-PESTLE

Fig. 49

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
1.	Thysanoptera (Permothripidae): *Tschekardus hispidus* Vishniakova	[89]	Vishniakova 1981
2.	Hoplopleuridae: *Neohaematopinus relictus* Dubinin	[Pleist]	Laurentiaux 1953
3.	Mallophaga, family indeterminate	[19]	Keilbach 1982
4.	Mallophaga, family indeterminate	[19]	Keilbach 1982
5.	Permopsocidae: *Permopsocus latipennis* Tillyard, Cyphoneuridae: *Cyphoneura* sp.	[90]	Tillyard 1926; Carpenter 1932
6.	Martynopsocidae: *Martynopsocus arcuatus* Martynov	[89]	Laurentiaux 1953
7.	Edgarriekiidae: *Edgarriekia uma* Jell & Duncan	[53]	Jell & Duncan 1986
8.	Dichentomidae: *Dichentomum tinctum* Tillyard	[90]	Tillyard 1926
9.	Dichentomidae: *Dichentomum soyanense* Bekker-Migdisova	[86]	Bekker-Migdisova 1940, 1961
10.	Dichentomidae: *Austropsocidium*, *Megapsocidium*, *Stenopsocidium*	[83]	Laurentiaux 1953
11.	Surijokopsocidae: *Surijokpsocus radtschenkovi* Bekker-Migdisova	[97]	Bekker-Migdisova 1961
12.	Archipsyllidae: *Eopsylla sojanensis* Bekker-Migdisova	[86]	Bekker-Migdisova 1940, 1961

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
13.	Archipsyllidae: *Archipsylla antiqua* Handlirsch	[68]	Laurentiaux 1953
14.	Archipsyllidae: *Archipsylla turanica* Martynov	[60]	Rasnitsyn 1988
15.	Archipsyllidae	[52]	Rasnitsyn 1988
16.	Trogiidae: *Eolepinotus pilosus* Vishniakova	[37]	Vishniakova 1975
17.	Lepidopsocidae	[17]	Schlee & Glockner 1978
18.	Lepidopsocidae	[11]	Baroni-Urbani & Saunders 1982
19.	Trogiidae: Empheiinae	[6]	Schumann & Wendt 1989
20.	Psyllipsocidae: *Khatangia includa* Vishniakova	[37]	Vishniakova 1975
21.	Psyllipsocidae: *Psyllipsocus ?banksi* Cockerell	[15]	Cockerell 1916; Rasnitsyn 1988
22.	Psyllipsocidae: *Psyllipsocus* sp.	[11]	Mockford 1969
23.	Liposcelidae: *Liposcelis* sp.	[33]	George 1969
24.	Sphaeropsocidae	[37]	Rasnitsyn 1988
25.	Liposcelidae: *Liposcelis atavus* Enderlien	[19]	Enderlein 1911
26.	Liooscelidae: *Belaphotroctes similis* Mockford	[11]	Mockford 1969
27.	Sphaeropsocidae: *Sphaeropsocus kuenowii* Hagen	[6]	Hagen 1882; Schumann & Wendt 1989
28.	Electroentomidae	[19]	Laurentiaux 1953
29.	Amphientomidae: *Proamphientomum cretaceum* Vishniakova	[37]	Vishniakova 1975
30.	Amphientomidae: *Amphientomum paradoxicum* Pictet	[19]	Pictet 1854; Keilbach 1982
31.	Amphientomidae: *Amphientomuka elongatum* Mockford	[11]	Mockford 1969
32.	Amphientomidae	[6]	Schumann & Wendt 1989
33.	Epipsocidae: *Epipsocus ciliatus* Pictet	[19]	Pictet-Baraban & Hagen 1956
34.	Epipsocidae: *Epipsocus clarus* Mockford	[11]	Mockford 1969
35.	Epipsocidae: *Epipsocus avus* Roesler	[6]	Schumann & Wendt 1989
36.	Caeciliidae: *Caecilius proavus* Hagen	[19]	Pictet-Baraban & Hagen 1856; Larsson 1978; Keilbach 1982
37.	Caeciliidae	[18]	Jarzembowski 1976
38.	Caeciliidae	[6]	Schumann & Wendt 1989
39.	Elipsocidae: *Cretapsocus capillatus* Vishniakova, Lachesillidae: *Archaelachesis granulosa* Vishniakova	[37]	Vishniakova 1975
40.	Elipsocidae: *Elipsocus abnormis* Hagen 1856 Philotarsidae: *Philotarsus antiquus* Kolbe, Archipsocidae: *Archipsocus puber* Hagen	[19]	Pictet-Baraban & Hagen 1856; Hagen 1882; Kolbe 1883
41.	Trichopsocidae: *Trichopsocus maculosus* Mockford Ectopsocidae: *Ectopsocus* sp.	[11]	Mockford 1969
42.	Peripsocidae	[6]	Schumann & Wendt 1989
43.	Psocidae: *Coptostigma affinis* Pictet, Myopsocidae	[11]	Pictet-Baraban & Hagen 1856; Mockford 1969
44.	Psocidae: *Coptostigma* sp.	[6]	Schumann & Wendt 1989

MOUTHPART CLASS 8: ROSTRATE

Fig. 52

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
1.	*Triassopsychops superba* Tillyard	[74]	Tillyard 1922
2.	*Beipiaopsychops triangulata* Hong	[64]	Hong 1983
3.	Psychopsidae	[57]	Whalley 1988
4.	*Propsychopsis helmi* Krüger	[19]	Krüger 1923; Larsson 1978
5.	*Marquettia americana* Cockerell	[15]	Cockerell 1907c; Carpenter 1960a
6.	Unnamed family: *Tarwinia australis* Jell & Duncan	[53]	Riek 1970a; Jell & Duncan 1986
7.	*Cyclochorista convexicosta* Martynova	[97]	Martynova 1958, 1961
8.	*Robinjohnia tillyardi* Martynova	[83]	Hennig 1981
9.	*Neorthophlebia robusta* Martynov	[71]	Martynova 1937a
10.	*Protobittacus arculatus* Bode	[68]	Bode 1953
11.	*Probittacus avitus* Martynov	[60]	Martynov 1927a; Rohdendorf 1968a
12.	Bittacidae	[52]	Rasnitsyn 1988
13.	Bittacidae	[23]	Grande 1980
14.	*Bittacus fossilis* Carpenter	[19]	Larsson 1978; Keilbach 1982
15.	*Bittacus veternus* (Cockerell)	[18]	Jarzembowski 1980
16.	Bittacidae	[15]	Wilson 1978a
17.	Boreidae	[L. Jura]	Rasnitsyn 1988
18.	*Tomiochorista nubila* Martynova	[97]	Martynova 1958, 1961
19.	*Platychorista venosa* Tillyard	[90]	Tillyard 1926b
20.	*Marimerobius splendens* Zalessky	[89]	Zalessky 1946
21.	*Thaumatomerope sogdiana* Rasnitsyn	[82]	Rasnitsyn 1974
22.	*Eomerope asiatica* Ponomarenko	[31]	Ponomarenko & Rasnitsyn 1974
23.	*Eomerope tortriciformis* Cockerell	[15]	Cockerell 1909d; Ponomarenko & Rasnitsyn 1974
24.	*Mesochorista proavita* Tillyard	[74]	Tillyard 1916; Riek 1955
25.	*Cretacochorista parva* Jell & Duncan	[53]	Jell & Duncan 1986
26.	*Dinopanorpa megarche* Cockerell	[12]	Cockerell 1925a
27.	*Orthophlebia angustata* Martynov	[71]	Martynov 1937a
28.	*Orthophlebia cappilata* Whalley	[69]	Whalley 1985
29.	*Protorthophlebia cuneata* Bode	[68]	Bode 1953
30.	*Protorthophlebia yaugouensis* Hong	[64]	Hong 1983
31.	*Orthophlebia grandis* Martynov	[60]	Martynov 1927a; Rohdendorf 1968a
32.	*Protorthophlebia* sp.	[57]	Jarzembowski 1984
33.	Orthophlebiinae	[54]	Sanz *et al.* 1988
34.	*Choristopanorpa drinnani* Jell & Duncan	[53]	Jell & Duncan 1986
35.	*Panorpodes* sp.	[19]	Larsson 1978
36.	Panorpidae	[15]	Wilson 1978a
37.	Panorpidae	[60]	Rasnitsyn 1988
38.	*Panorpa obsoleta* Carpenter	[19]	Larsson 1978; Keilbach 1982
39.	Panorpidae	[15]	Wilson 1978a

CLASS 10: RHYNCHOPHORATE

Fig. 55

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
1.	Cerambycidae: *Parandrexis beipiaoensis* Hong	[64]	Hong 1983
2.	Nemonychidae	[60]	Rasnitsyn 1988
3.	Nemonychidae	[52]	Rasnitsyn 1988
4.	Nemonychidae	[19]	Crowson 1976
5.	Anthribidae	[E. Cret]	Rasnitsyn 1988
6.	Anthribidae	[52]	Dmitriev & Zherikin 1988
7.	*Pseudomecorhis simulator* Voss	[19]	Larsson 1978
8.	*Saperdirhynchus priscotitillator* Scudder	[15]	Scudder 1893; Wilson 1978a
9.	*Archaeorhynchus latitarsus* Arnoldi	[60]	Arnoldi 1977
10.	*Eobelus solutus* Whalley & Jarzembowski	[56]	Whalley & Jarzembowski 1985
11.	*Ampliceps dentibia* Arnoldi	[60]	Arnoldi 1977
12.	*Paltorhynchus* sp.	[23]	Crowson 1976
13.	Oxycoronidae	[19]	Crowson 1976
14.	Oxycoronidae	[?17]	Dmitriev & Zherikin 1988
15.	*Baissorhynchus tarsalis* Zherikin	[52]	Zherikin 1977
16.	Attelabidae	[23]	Wilson 1978a; Grande 1980
17.	*Rhynchites subterraneus* Scudder	[15]	Wickham 1913; Wilson 1978a
18.	*Cretonanophyes longirostris* Zherikin	[60]	Zherikin 1977
19.	Apionidae ("probably")	[43]	McKay & Ratner 1986
20.	*Apion andersi* Voss	[19]	Larsson 1978; Keilbach 1982
21.	Curculionidae	[69]	Whalley 1985
22.	*Slonik sibiricus* Zherikin	[60]	Zherikin 1977
23.	*Curculionites hylobiodes* Northrup	[50]	Northrup 1928
24.	*Dorotheus guidensis* Kuschel	[Mastric]	Kuschel 1959
25.	*Otiorhynchites wilcoxianus* Wickham	[25]	Wickham 1929
26.	*Pissodites argillosus* Britton	[26]	Britton 1960
27.	*Cryptorrhynchites sculpturatus* Haupt	[22]	Haupt 1950
28.	*Cryphalites rugosissimus* Cockerell	[19]	Keilbach 1982
29.	*Geralophus antiquarius* Scudder	[15]	Wickham 1913
30.	*Ceutorhynchus* sp.	[1]	Hopkins *et al.* 1971

MOUTHPART CLASS 10: PECTINATE

Fig. 58

1.	Protorthoptera (Paoliidae): *Ampeliptera limburgica* Pruvost	[100]	Pruvost 1927; Brauckmann 1988
2.	Meganeuridae: *Erasipteroides valentini* Brauckmann	[99]	Brauckmann *et al.* 1985
3.	Triplosobidae: *Triplosoba pulchella* Brongniart	[95]	Brongniart 1893; Crowson *et al.* 1967
4.	Syntopoteridae: *Lithoneura piecko* Kukalová-Peck, Bojophlebiidae: *Bojophlebia prokopi* Kukalová-Peck	[96]	Kukalová-Peck 1985
5.	Misthodotidae: *Misthodotes stapfi* Kinzelbach & Lutz	[94]	Kinzelbach & Lutz 1984
6.	Kukaloviidae: *Oboriphlebia moravica* (Demoulin)	[92]	Demoulin 1970
7.	Protereismidae: *Protereisma permianum* Sellards	[90]	Sellards 1907; Crowson *et al.* 1967

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
8.	Misthodotidae: *Misthodotes zalesskyi* Chernova	[89]	Chernova 1965
9.	Protereismidae: *Palingeniopsis praecox* Martynov	[86]	Martynov 1932
10.	Mesoplectopteridae: *Mesoplectopteron longipes*	[81]	Handlirsch 1918
11.	Palingeniidae: *Mesogenesia petersae* Chernova, Behningiidae: *Archaeobehningia edmundsi* Chernova	[62]	Chernova 1977
12.	Palingeniidae: *Mesopalingenia lerida* Whalley &	[56]	Whalley & Jarzembowski 1985
13.	Potamanthidae: *Potamanthus* sp., Ephemeridae	[19]	Keilbach 1982
14.	Ephemeridae: *Ephemera* sp.	[15]	Chernova 1970
15.	Mesephemeridae: *Mesephemera cellulosa* Hagen	[61]	Hagen 1862; Kuhn 1961
16.	Leptophlebiidae: *Mesoneta antiqua* Brauer, Redtenbacher & Ganglbauer	[64]	Brauer *et al.* 1989; Hong 1983
17.	Leptophlebiidae	[54]	Sanz *et al.* 1988
18.	Leptophlebiidae: *Cretoneta zherichini* Chernova	[37]	Chernova 1971
19.	Leptophlebiidae: *Paraleptophlebia prisca* (Pictet)	[19]	Pictet-Barraban & Hagen 1856; Keilbach 1982
20.	?Leptophlebioidea	[6]	Schumann & Wendt 1989
21.	Leptophlebiidae: *Atalophlebia culleni* Etheridge & Oliff	[Plioc]	Etheridge & Oliff 1890; Riek 1954
22.	Heptageniidae: *Electrogenia dewalschei* Demoulin	[19]	Demoulin 1956a; Keilbach 1982
23.	Siphlonuridae: *Mesobaetis sibirica* Brauer, Redtenbacher & Ganglbauer	[67]	Brauer *et al.* 1989; Cockerell 1924
24.	Siphlonuridae: *Stackelbergisca sibirica* Chernova	[62]	Chernova 1967
25.	Siphlonuridae: *Mesonetopsis zein* Ping	[L. Jura]	Ping 1935; Edmunds 1972
26.	Siphlonuridae: *Promirava cephalota* Jell & Duncan	[53]	Jell & Duncan 1986
27.	Siphlonuridae: *Proameletus caudatus* Sinichenkova	[52]	Sinichenkova 1976
28.	Isonychidae	[37]	Zherikin & Sukacheva 1973
29.	Ametropidae: *Siphloplecton macrops* (Pictet)	[19]	Keilbach 1982
30.	Siphlonuridae: *Siphlurites* sp.	[15]	Chernova 1970
31.	?Baetidae	[6]	Schumann & Wendt 1989
32.	Baetidae: *Cloeon emmavillensis* Riek	[Plioc]	Riek 1954
33.	?Oligoneuridae	[19]	Chernova 1980
34.	Hexagenitidae: *Ephemeropsis trisetalis* Eichwald	[64]	Lin 1976
35.	Hexagenitidae: *Hexagenites weyenberghi* Carpenter	[61]	Carpenter 1932; Kuhn 1961
36.	Aenigmaephemeridae: *Aenigmaephemera demoulini* Chernova	[60]	Chernova 1968
37.	Hexagenitidae: *Ephemeropsis trisetalis* Eichwald	[52]	Sinichenkova 1975
38.	Ephemerellidae: *Turfanerella tingi* Ping	[L Jura]	Ping 1935; Edmunds 1972
39.	Ephemerellidae: *Ephemerella viscata* Demoulin	[19]	Demoulin 1968; Keilbach 1982

MOUTHPART CLASS 11: MOUTHBRUSH
Fig. 61

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
1.	Protomeropeidae: *Altajopanorpa pilosa* Martynova	[66]	Martynova 1959, 1961
2.	Unnamed family: *Tarwinia australis* Jell & Duncan	[53]	Riek 1970a; Jell & Duncan 1986
3.	Dictyodipteridae: *Dictyodiptera multinervis*	[73]	Rohdendorf 1961, 1974
4.	*Eotrichocera christinae* Kalugina	[66]	Kalugina & Kovalev 1985
5.	*Mailotrichocera jurassica* Kalugina	[62]	Kalugina & Kovalev 1985
6.	Trichoceridae	[60]	Rasnitsyn 1988
7.	Trichoceridae	[52]	Rasnitsyn 1988
8.	*Oligotrichocera antiqua* (Loew)	[19]	Loew 1850; Keilbach 1982
9.	*Trichocera oligocaenica* Statz	[8]	Statz 1944b
10.	*Trichocera* sp.	[6]	Schumann & Wendt 1989
11.	Tipulidae	[76]	Olsen *et al.* 1978
12.	*Tipuloidea rhaetica* Wieland	[Norian]	Wieland 1925
13.	*Dictyotipula densa* Rohdendorf	[73]	Rohdendorf 1962b, 1974
14.	*Architipula simplex* Handlirsch	[68]	Handlirsch 1939
15.	*Eotipulina sibirica* Kalugina	[66]	Kalugina & Kovalev 1985
16.	*Eotipulina fumosa* Kalugina	[65]	Kalugina & Kovalev 1985
17.	*Sinotipula huabeiensis* Hong	[64]	Hong 1983
18.	*Eotipuloptera sautshenkovi* Kalugina	[62]	Kalugina 1985
19.	Limoniinae	[60]	Rasnitsyn 1988
20.	*Corethrium pertinax* Westwood	[59]	Westwood 1854; Rohdendorf 1974
21.	Aff. *Gynoplistia*	[57]	Jarzembowski 1984
22.	Limoniinae indet.	[53]	Jell & Duncan 1986
23.	Limoniinae	[52]	Rasnitsyn 1988
24.	Limoniinae	[42]	Rasnitsyn 1988
25.	Tipulidae	[37]	Zherikin & Sukacheva 1973
26.	*Limnophila* sp.	[32]	Mitchell & Wighton 1979
27.	Tipulidae	[24,23]	Wilson 1978a; Lutz 1987
28.	*Limonia deleta* Giebel	[19]	Giebel 1856; Keilbach 1982
29.	*Tipula limiformis* Cockerell	[18]	Cockerell 1916b
30.	Tipulidae	[17]	Schlee & Glockner 1978
31.	*Tipula wilmatteae* Melander	[15]	Melander 1949
32.	Tipulidae; *Tipula carpenteri* Alexander	[12,11]	Carpenter *et al.* 1937; Alexander & Byers 1981
33.	*Tipula sectoralis*; *Helius tenera* Statz	[11,8]	Zeuner 1938; Statz 1944b
34.	*Rhabdomastix elegantula* Meunier	[6]	Meunier 1906; Schumann & Wendt 1989
35.	*Tipulodictya minima* Rohdendorf	[73]	Rohdendorf 1962
36.	Blepharoceridae	[42]	Rasnitsyn 1988
37.	?*Paltostomopsis ciliatus*	[18]	Cockerell 1916b
38.	*Praemacrochile stackelbergi* Kalugina	[66]	Kalugina & Kovalev 1985
39.	Tanyderidae	[60]	Rasnitsyn 1988
40.	*Macrochile spectrum* Loew	[19]	Loew 1851; Crampton 1926
41.	*Eolimnobia geinitzi* Handlirsch	[68]	Handlirsch 1908
42.	Eoptychopteridae	[60]	Rasnitsyn 1988
43.	*Bolboia mira* Kalugina	[58]	Kalugina 1989
44.	Eoptychopteridae	[52]	Rasnitsyn 1988

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
45.	*Ptychoptera mesozoica* Kalugina	[52]	Kalugina 1989
46.	Ptychopteridae	[32]	Wilson 1978a
47.	*Bittacomorphella miocaenica* Cockerell	[15]	Alexander 1981c
48.	*Ptychoptera deleta* Novak	[8]	Alexander 1981c
49.	*Mesopsychoda dasyptera* Brauer, Redtenbacher & Ganglbauer	[67]	Brauer *et al.* 1889
50.	*Eopericoma zherichini* Kalugina	[62]	Kalugina & Kovalev 1985
51.	*Tanyderophryne multinervis* Rohdendorf	[60]	Rohdendorf 1962, 1974
52.	*Phlebotomites brevifilis* Hennig	[55]	Hennig 1972b
53.	*Sycorax* sp.	[35]	Quate & Vockeroth 1981
54.	*Nemopalpus molophinus* Edwards	[19]	Keilbach 1982
55.	Psychodidae	[18]	Jarzembowski 1976
56.	*Nemopalpus henningianus* Schlüter	[17]	Baroni-Urbani & Saunders 1982
57.	*Trichomyia antiquaria* Quate	[11]	Quate 1961
58.	Psychodidae	[6]	Schumann & Wendt 1989
59.	Thaumaleidae	[E. Cret]	Rasnitsyn 1988
60.	Simuliidae	[60]	Rasnitsyn 1988
61.	Simuliidae	[53]	Jell & Duncan 1986
62.	*Simulium importunum* Meunier	[19]	Keilbach 1982
63.	Simuliidae	[10]	Cuffey *et al.* 1982
64.	Simuliidae	[6]	Schumann & Wendt 1989
65.	Ceratopogonidae	[55]	Schlee & Dietrich 1970
66.	?*Forcipomyia* sp.	[45]	Schlüter 1978
67.	*Culicoides kaluginae* Remm	[37]	Remm 1976
68.	?*Culicoides casei* Grogan & Szadziewski	[36]	Grogan & Szadziewski 1988
69.	*Lasiohelia creta* Boesel	[35]	Boesel 1937
70.	*Ceratopogon flagellus* Meunier	[19]	Meunier 1904d; Keilbach 1982
71.	Ceratopogonidae	[17]	Schlee & Glockner 1978
72.	Ceratopogonidae	[10]	Cuffey *et al.* 1982
73.	*Culicoides obscuratus* Statz	[8]	Statz 1944c
74.	*Atrichopogon* sp.	[6]	Schumann & Wendt 1989
75.	*Dasyhelea australis* Palmer	[4]	Palmer 1957
76.	*Architendipes tschnernovskii*	[73]	Rohdendorf 1974
77.	Chironomidae	[66]	Kalugina 1983
78.	?*Podonomus rotundatus* Kalugina	[65]	Kalugina & Kovalev 1985
79.	*Oryctochlus vulcanus* Kalugina	[62]	Kalugina & Kovalev 1985
80.	?*Protendipes* sp.	[60]	Kalugina & Kovalev 1985
81.	*Libinoclites neocomicus* Brundin	[55]	Brundin 1976
82.	Tanypodinae	[53]	Jell & Duncan 1986
83.	*Cretodiamesa taimyrica* Kalugina	[37]	Kalugina 1976
84.	?*Tventenia* sp.	[36]	Grimaldi *et al.* 1989
85.	*Smittia veta* Boesel	[35]	Boesel 1937
86.	Chironomidae	[24]	Lutz 1987
87.	Chironomidae	[23]	Wilson 1978a
88.	*Chironomus obscuratus* Meunier	[19]	Meunier 1899; Larsson 1978
89.	Chironomidae	[17]	Schlee & Glockner 1978
90.	*Chironomus pristinus* Melander; "larves"	[15,13]	Théobald 1937; Melander 1949

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
91.	Chironomidae	[10]	Cuffey *et al.* 1982
92.	*Pelopia thienemanni* Statz	[8]	Statz 1944b
93.	Chironomidae	[6]	Schumann & Wendt 1989
94.	*Calopsectra* sp.	[4]	Palmer 1957
95.	*Praechaoborus tugnuicus* Kalugina	[66]	Kalugina & Kovalev 1985
96.	*Eucorethrina flexa* Kalugina	[65]	Kalugina & Kovalev 1985
97.	*Chironomaptera robustus* Lin	[64]	Lin 1976
98.	*Chironomaptera scobloi* Kalugina	[62]	Kalugina & Kovalev 1985
99.	*Chironomaptera collessi* Jell & Duncan	[53]	Jell & Duncan 1986
100.	*Chaoborus tertiarius* (Von Heyden)	[22]	Cook 1981
101.	*Mochlonyx atavus* Loew	[19]	Loew 1861; Larsson 1978
102.	*Chaoborus* sp.	[13]	Cook 1981
103.	?Chaoboridae	[Miocene]	Scudder 1890
104.	Chaoboridae	[6]	Schumann & Wendt 1989
105.	?Culicidae	[57]	Jarzembowski 1984
106.	Culicidae	[23]	Wilson 1978a
107.	*Culex pipiens* Linneaus	[19]	Keilbach 1982
108.	*Culex protolepis* Cockerell	[18]	Cockerell 1916b
109.	Culicidae	[17]	Schlee & Glockner 1978
110.	Culicidae; *Culicites depereti* Meunier	[11,10]	Wilson 1978a; Lutz 1985
111.	Culicidae	[10]	Cuffey *et al.* 1982
112.	*Anopheles rottensis* Statz	[8]	Statz 1944b
113.	Dixidae	[53]	Jell & Duncan 1986
114.	*Paradixa succinea* Meunier	[19]	Meunier 1906b; Hennig 1966
115.	Dixidae	[6]	Schumann & Wendt 1989
116.	Pachyneuridae	[60]	Rasnitsyn 1988
117.	Pachyneuridae	[17]	Schlee & Glockner 1978
118.	Paraxymyiidae	[Lias]	Dmitriev & Zherikin 1988
119.	*Arius beiopiaoensis* Hong	[64]	Hong 1983
120.	*Paraxymyia quadriradialis* Rohdendorf	[60]	Rohdendorf 1946
121.	*Palaeoperissosomma collessi* Kovalev	[65]	Kalugina & Kovalev 1985
122.	Perissosommatidae	[Dogger]	Dmitriev & Zherikin 1988
123.	*Protolbiogaster rhaetica* Rohdendorf	[73]	Rohdendorf 1974
124.	*Protoplecia liasina* (Geinitz)	[68]	Geinitz 1884; Peterson 1975
125.	*Archipleciomima longicornis* Kovalev	[66]	Kalugina & Kovalev 1985
126.	*Mesoplecia jurassica* Rohdendorf	[60]	Rohdendorf 1938
127.	*Simulidium priscum* Westwood	[59]	Westwood 1854; Rohdendorf 1974
128.	Protopleciidae	[Albian]	Dmitriev & Zherikin 1988
129.	Bibionidae	[76]	Olsen *et al.* 1978
130.	?*Beipiaoplecia malleformis* Lin	[64]	Lin 1976
131.	Bibionidae	[52]	Rasnitsyn 1988
132.	Bibionidae	[43]	Rayner 1987
133.	?Bibionidae	[37]	Zherikin & Sukacheva 1973
134.	Bibionidae	[35]	McAlpine & Martin 1969
135.	Bibionidae	[32]	Wilson 1978a
136.	Bibionidae	[23]	Wilson 1978a
137.	*Plecia crassicornis* Loew	[19]	Loew 1850; Keilbach 1982
138.	*Bibiodites confluens* Cockerell	[18]	Cockerell 1916b

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
139.	*Hesperinus immutabilis* Melander,	[15,13]	Melander 1949; Théobald 1937
140.	*Plecia amagua*; *Plecia pristina* Hardy	[12,11]	Cockerell 1925a; Hardy 1971
141.	*Bibio sticheli* Handlirsch	[9]	Handlirsch 1908; Zeuner 1938
142.	*Rhaetofungivora reticulata* Rohdendorf	[73]	Rohdendorf 1962
143.	*Rodendorfomyiella incorporalis* Kovalev	[66]	Kalugina & Kovalev 1985
144.	*Bryanska elegantissima* Kovalev	[65]	Kalugina & Kovalev 1985
145.	*Williheunigia curtipes* Kovalev	[62]	Kalugina & Kovalev 1985
146.	Pleciofungivoridae	[60]	Rasnitsyn 1988
147.	Pleciofungivoridae	[52]	Rasnitsyn 1988
148.	*Protoscatopse jurassica*	[60]	Rohdendorf 1946
149.	Scatopsidae	[42]	Rasnitsyn 1988
150.	*Prohyperoscelis jurassicus* Kovalev	[65]	Kalugina & Kovalev 1985
151.	*Prodocidia spectra* Whalley	[69]	Whalley 1985
152.	Sciophilinae	[57]	Jarzembowski 1984
153.	*Pseudalysiinia fragmenta* Jell & Duncan	[53]	Jell & Duncan 1986
154.	Mycetophilidae	[52]	Rasnitsyn 1988
155.	*Schlueterimyia cenomanica* Matile	[45]	Matile 1981
156.	Mycetophilidae	[42]	Rasnitsyn 1988
157.	Mycetophilidae	[37]	Zherikin & Sukacheva 1973
158.	Mycetophilidae	[36]	Grimaldi *et al.* 1989
159.	Sciophilinae	[35]	McAlpine & Martin 1969
160.	Mycetophilidae	[32]	Wilson 1978a
161.	Mycetophilidae	[23]	Wilson 1978a
162.	*Mycetophila antennata* (Loew)	[19]	Loew 1850; Keilbach 1982
163.	*Mycetophila vectensis* Cockerell	[18]	Cockerell 1916b
164.	*Proceroplatus hennigi* Schmalfuss	[17]	Schmalfuss 1979; Keilbach 1982
165.	*Exechia priscula* Melander	[15]	Melander 1949
166.	Mycetophilidae	[8]	Statz 1944a
167.	Mycetophilidae	[6]	Schumann & Wendt 1989
168.	Sciaridae	[55]	Grimaldi *et al.* 1989
169.	Sciaridae	[52]	Rasnitsyn 1988
170.	Sciaridae	[42]	Rasnitsyn 1988
171.	*Sciara* cf. *deflectuosa* Meunier	[36]	Grimaldi *et al.* 1989
172.	Sciaridae	[35]	McAlpine & Martin 1969
173.	Sciaridae	[32]	Wilson 1978a
174.	*Sciara* sp.	[23]	Wilson 1978a
175.	*Heterotricha hirta* (Loew)	[19]	Loew 1850; Keilbach 1982
176.	*Sciara gurnetensis* cockerell	[18]	Cockerell 1916b
177.	Sciaridae	[17]	Baroni-Urbani & Saunders 1982
178.	*Sciara sopora* Melander; *Sciara* sp.	[15,13]	Théobald 1937; Melander 1949
179.	*Sciara meylandi*	[8]	Statz 1944
180.	Sciaridae	[6]	Schumann & Wendt 1989
181.	Cecidomyiidae	[55]	Schlee & Dietrich 1970; Gagné 1973
182.	Brachycera (Protobrachyceronidae): *Protobrachyceron* Handlirsch	[68]	Handlirsch 1908; Kalugina & Kovalev 1985
183.	Dryopoidea	[69]	Whalley 1985
184.	Buprestidae	[76]	Olsen *et al.* 1978
185.	Buprestidae: *Pseudothyrea oppenheimi* Handlirsch	[61]	Ponomarenko 1971

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
186.	Buprestidae	[60]	Crowson 1981; Rasnitsyn 1988
187.	Buprestidae: ?*Chrysobotris ballae* Whalley & Jarzembowski	[56]	Whalley & Jarzembowski 1985
188.	Buprestidae	[52]	Rasnitsyn 1988
189.	Buprestidae	[39]	Rasnitsyn 1988
190.	Buprestidae	[32]	Wilson 1978a
191.	Buprestidae	[24]	Lutz 1987
192.	Buprestidae: *Chlorodema primordalis* (Pongracz)	[22]	Haupt 1950; Abdullah 1975
193.	Buprestidae: *Electrapate martynovi* Yablokov-Kinzorian	[19]	Yablokov-Kinzorian 1962; Keilbach 1982
194.	Buprestidae: *Buprestus florissantensis* Wickham	[15]	Wickham 1914
195.	*Prolyonetia cockerelli* Kusnezov	[19]	Kusnezov 1941; Kozlov 1988b
196.	*Bucculatrix platani* Kozlov, leaf-mine on *Platanus*	[39]	Kozlov 1988b
197.	*Gracillarites* sp., leaf-mine	[29]	Crane & Jarzembowski 1980; Kozlov 1988b
198.	*Gracillarites lithuanicus* Kozlov	[19]	Kozlov 1987
199.	*Lithocolletis* sp., leaf-mine on unknown leaf	[Miocene]	Freeman 1965
200.	*Bucculatrix platanus* Kozlov, leaf-mine on *Platanus*	[Miocene]	Kozlov 1988b
201.	*Caloptilia* sp., leaf-mine on *Quercus*	[Miocene]	Opler 1973
202.	*Caloptilia* sp., leaf-mine on *Quercus*	[Miocene]	Opler 1973
203.	*Phyllocnistis* sp., leaf-mine on *Cedrela*	[23]	Hickey & Hodges 1975

MOUTHPART CLASS 12: MANDIBULOBRUSTIATE

Fig. 64

1.	Archaeolepidae: *Archaeolepis mane* Whalley	[69]	Whalley 1985, 1986
2.	*Electralberta cretacica* Botosaneanu & Wichard	[35]	Botosaneanu & Wichard 1983
3.	Psychomyiidae	[34]	Wolbert *et al.* 1988
4.	*Archaeotinodes lanceolata* Ulmer	[19]	Keilbach 1982
5.	*Hydropsyche submaculata* Kolenati	[19]	Keilbach 1982
6.	*Leptonema* sp.	[17]	Wichard 1987
7.	Hydropsychidae	[15]	Wilson 1978a
8.	*Archaeopolycentra zherikhini* Botosaneanu & Wichard	[37]	Botosaneanu & Wichard 1983
9.	*Antillopsyche* sp.	[17]	Wichard 1987
10.	*Prephilopotamus asiaticus* Sukacheva	[82]	Sukacheva 1973
11.	Philopotamidae	[37]	Botosaneanu & Wichard 1983
12.	*Chimarra succini* Wichard	[17]	Wichard 1983
13.	*Necrotaulius proximus* Sukacheva	[70]	Sukacheva 1973
14.	*Necrotaulius marginatus* Bode	[68]	Bode 1953
15.	*Necrotaulius fascialatus* Hong	[64[	Hong 1983
16.	*Karataulius aeternus* Sukacheva	[60]	Sukacheva 1968b
17.	Rhyacophilidae	[L. Jura]	Dmitriev & Zherikin 1988
18.	*Rhyacophila antiquissima* Botosaneanu & Wichard	[37]	Botosaneanu & Wichard 1983
19.	*Rhyacophila kutscheri* Mey	[19]	Mey 1988
20.	Glossosomatidae	[19]	Dmitriev & Zherikin 1988
21.	*Campsiophora* sp.	[17]	Wichard 1987

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
22.	*Palaeohydrobiosis siberambra* (Botosaneanu & Wichard	[37]	Botosaneanu & Wichard 1982
23.	Hydroptilidae	[37]	Dmitriev & Zherikin 1988
24.	Hydroptilidae	[23]	Wilson 1978a
25.	*Agraylea spathifera* Ulmer	[19]	Larsson 1978; Keilbach 1982
26.	*Alisotrichia* sp.	[17]	Wichard 1987
27.	Hydroptilidae	[15]	Wilson 1978a
28.	*Prorhyacophila furcata* Sukacheva	[70]	Sukacheva 1973
29.	*Dysoneura trifurcata* Sukacheva	[60]	Sukacheva 1968b
30.	*Baissophryganoides monstruosus* Sukacheva	[52]	Sukacheva 1968a
31.	Phryganeidae	[15]	Wilson 1978a
32.	*Phryganea lavrushini* Cockerell	[12]	Cockerell 1925a
33.	*Baissoferus latus* Sukacheva	[52]	Sukacheva 1968a
34.	Lepidosomatidae	[19]	Dmitriev & Zherikin 1988
35.	Limnephilidae	[15]	Wilson 1978a
36.	*Limnephilus recultus* Cockerell	[12]	Cockerell 1925a
37.	*Goera gracilicornis* Ulmer	[19]	Keilbach 1982
38.	*Brachycentrus labialis* Hagen	[19]	Pictet-Baraban & Hagen 1856; Keilbach 1982
39.	Vitimotaulidae	[60]	Rasnitsyn 1988
40.	*Vitimotaulius legibilis* Sukacheva	[52]	Sukacheva 1968a
41.	*Beraeodes pectinata* Ulmer	[19]	Keilbach 1982
42.	Sericostomatidae	[37]	Zherikin & Sukacheva 1973
43.	*Arachaeocrunoecia valdicornis* Ulmer	[19]	Keilbach 1982
44.	Sericostomatidae	[15]	Wilson 1978a
45.	Odontoceridae	[15]	Wilson 1978a
46.	*Molanna crassicornis* Ulmer	[19]	Larsson 1978; Keilbach 1982
47.	Helicopsychidae	[19]	Dmitriev & Zherikin 1988
48.	*Helicopsyche* sp.	[17]	Wichard 1987
49.	?*Oecetis* sp.	[53]	Jell & Duncan 1986
50.	*Praeathripsodes jantar* Botosaneanu & Wichard	[37]	Botosaneanu & Wichard 1983
51.	*Nectopsyche* sp.	[17]	Wichard 1983
52.	Leptoceridae	[15]	Wilson 1978a
53.	Calamoceratidae	[53]	Jell & Duncan 1986
54.	*Rhabdoceras fusculus* Ulmer	[19]	Larsson 1978; Keilbach 1982

MOUTHPART CLASS 13: SERICTERATE

Fig. 67

1.	Coleoptera (Cupedidae): *Eocupes lukjanovitschi* Rohdendorf, and several other families	[97]	Rohdendorf 1961
2.	Megaloptera (Permosialidae): *Permosialis sibirica* Martynova; Planipennia (Permithionidae): *Permithonopsis kaltanensis* Martynova	[97]	Martynova 1961; Crowson *et al.* 1967
3.	Xyelidae: *Triassoxyela foveolata* Rasnitsyn	[82]	Rasnitsyn 1964
4.	Xyelididae: *Sagulyda ferganica* Rasnitsyn	[71]	Rasnitsyn 1983
5.	Xyelidae: *Liadoxyela iensis* Rasnitsyn	[67]	Rasnitsyn 1969

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
6.	Xyelidae: *Xyelisca leptopoda* Rasnitsyn	[66]	Rasnitsyn 1969
7.	Xyelididae: *Mesolyda depressa* Rasnitsyn	[60]	Rasnitsyn 1969
8.	Xyelidae: *Eoxyela sibirica* Rasnitsyn	[52]	Rasnitsyn 1969
9.	Pamphilidae: *Atocus defessus* Scudder	[15]	Scudder 1892
10.	Xyelotomidae: *Xyelotoma nigricornis* Rasnitsyn	[60]	Rasnitsyn 1968
11.	Xyelotomidae: *Vitimlarva paradoxa* Rasnitsyn	[52]	Rasnitsyn 1969
12.	Tenthredinidae	[15]	Wilson 1978a
13.	Myrmiciidae: *Shurabisca liassica* Rasnitsyn, Gigasiricidae: *Liasirex sogdianus* Rasnitsyn, Sepulcidae: *Sepulia mirabilis* Rasnitsyn	[71]	Rasnitsyn 1968
14.	Beipiaosiricidae: *Beipiaosirex parva* Hong, Sinoryssidae: *Sinoryssus suni* Hong	[64]	Hong 1983
15.	Siricidae: *Pseudosirex snelleni* Weyenbergh	[61]	Weyenberg 1869; Kuhn 1961
16.	Gigasiricidae: *Protosirex xyelopterus* Rasnitsyn	[60]	Rasnitsyn 1968
17.	Myrmiciidae: *Formicium brodiei* Westwood	[59]	Westwood 1854
18.	Syntexidae: *Dolichostigma tenuipes* Rasnitsyn	[52]	Rasnitsyn 1968
19.	Orussidae: *Mesorussus taimyrensis* Rasnitsyn	[37]	Rasnitsyn 1977a
20.	Myrmiciidae: *Megapterites mirabilis* Cockerell	[24]	Cockerell 1920
21.	Siricidae: *Urucerus klebsi* Brues	[19]	Brues 1926
22.	Siricidae	[15]	Wilson 1978a
23.	Cephidae: *Sinocephus beipaioensis* Hong	[64]	Hong 1983
24.	Cephidae: *Mesocephus sibiricus* Rasnitsyn	[69]	Rasnitsyn 1968
25.	Cephidae: *Electrocephus stralendorffi* Konow	[19]	Konow 1897
26.	Cephidae	[15]	Wilson 1978a
27.	Ichneumonidae: *Tanychorella parvula* Rasnitsyn	[66]	Rasnitsyn 1975
28.	Ichneumonidae: *Eoichneumon duncanae* Jell & Duncan	[53]	Jell & Duncan 1986
29.	Ichneumonidae: *Tanychora petiolata* Townes	[52]	Townes 1973a
30.	Ichneumonidae: *Catachora minor* Townes, Braconidae: *Diospilus allani* Brues	[37]	Brues 1937; Townes 1973b
31.	Ichneumonidae	[35]	McAlpine & Martin 1969
32.	Ichneumonidae	[33]	George 1952
33.	Ichneumonidae	[24]	Lutz 1987
34.	Braconidae: *Palaeorhyssalus dubitosus* Brues	[19]	Brues 1933
35.	Ichneumonidae; Ichneumonoidea	[18,17]	Jarzembowski 1976; Schlee & Glockner 1978
36.	Ichneumonidae	[15]	Wilson 1978a
37.	Trigonalidae: *Cretogonalys taimyricus* Rasnitsyn	[37]	Rasnitsyn 1977a
38.	Megalyridae: *Cleistogaster buriatica* Rasnitsyn	[66]	Rasnitsyn 1975
39.	Megalyridae: *Cleistogaster obscura* Rasnitsyn	[60]	Rasnitsyn 1975
40.	Ephialtitidae: *Ephialtites jurassicus* Meunier	[56]	Meunier 1903; Whalley & Jarzembowski 1985
41.	Megalyridae: *Cretogaster vitimica* Rasnitsyn	[52]	Rasnitsyn 1975
42.	Megalyridae: *Cretodinaspis caucasica* Rasnitsyn	[51]	Rasnitsyn 1977a
43.	Stephanidae: *Electrostephanus brevicornis* Brues, Megalyridae: *Prodinspsis succinalis* Brues	[19]	Brues 1923
44.	Stephanidae: *Protostephanus ashmeadi* Cockerell	[15]	Cockerell 1906; Brues 1910
45.	Megaspilidae: *Allocotidus bruesi* Muesebeck	[40]	Muesebeck 1963
46.	Heloridae: *Protohelorus mesozoicus* Kozlov	[60]	Kozlov 1968

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
47.	Mymaridae: *Galloromma bezonnaisensis* Schlüter	[45]	Schlüter 1978
48.	Ibalidae	[39]	Rasnitsyn 1980
49.	Cynipidae	[37]	Zherikin & Sukacheva 1973
50.	Cynipidae: *Protimaspis costalis* Kinsey	[35]	Kinsey 1937
51.	Cynipidae: *Aulacidea succinea* Kinsey	[19]	Kinsey 1919
52.	Cynipidae: *Rhodites vetus* Cockerell	[18]	Cockerell 1921
53.	Ibalidae: *Protoibalia connexiva* Brues, Figitidae: *Figites solus* Brues	[15]	Brues 1910
54.	Cynipoidea	[8]	Statz 1938
55.	Aulacidae: *Mesaulacinus oviformis* Martynov	[60]	Martynov 1925
56.	Aulacidae: *Paraulacus sinicus* Ping	[L. Jura/ E. Cret]	Ping1928
57.	Cretevaniidae	[57]	Jarzembowski 1984
58.	Cretevaniidae: *Cretevania minuta* Rasnitsyn, Aulacidae: *Mesaulacinus* sp., Evaniidae: Cleistogastrinae	[37]	Rasnitsyn 1975
59.	Evaniidae: *Evania remanea* Brues	[19]	Brues 1933
60.	Aulacidae: *Micraulacinus prisculus* Brues, Praeaulacidae, Evaniidae	[15]	Brukes 1910; Rasnitsyn 1972
61.	?Bethyloid	[53]	Jell & Duncan 1986
62.	Dryinidae: *Cretodryinus zherichini* Ponomarenko, Scolebythidae: *Cretabythus sibiricus* Evans, Chrysididae: *Hypocleptes rasnitsyni* Evans, Bethylidae: *Archepyris minutus* Evans	[37]	Evans 1973; Rasnitsyn 1975
63.	Chrysididae: *Procleptes carpentieri* Evans	[35]	Evans 1969
64.	Chrysididae: *Protochrysis succinalis* Bischoff, Embolemidae: *Embolemus breviscaptus* Brues	[19]	Bischoff 1915; Brues 1933
65.	Chrysididae: ?*Epyris tenellus* Statz	[8]	Statz 1938
66.	Pompilidae: *Pompiliopterus ciliatus* Rasnitsyn	[52]	Rasnitsyn 1975
67.	Pompilidae: *Epipompilius* sp.	[19]	Koningsmann 1978b
68.	Pompilidae: *Psammochares* sp.	[8]	Statz 1938
69.	Mutillidae: *Cretavus sibiricus* Sharov	[Cenoman]	Sharov 1957a; Hennig 1981
70.	Tiphiidae	[37]	Zherikin & Sukacheva 1973
71.	Mutillidae: *Protomutilla*, sp., Sapygidae	[19]	Bischoff 1927; Brothers 1974
72.	Tiphiidae: *Lithotiphia* sp.	[15]	Handlirsch 1908
73.	Angarosphecidae: *Angarosphex myrmicopterus* Rasnitsyn	[52]	Rasnitsyn 1975
74.	Falsiformicidae	[45]	Schlüter 1978
75.	Falsiformicidae: *Falsiformica cretacea* Rasnitsyn	[37]	Rasnitsyn 1975
76.	Masaridae: *Curiovespa curiosa* Rasnitsyn	[39]	Rasnitsyn 1975
77.	Eumenidae: ?*Alastor solidescens* (Scudder)	[27]	Piton 1940; Burnham 1978
78.	Vespidae: *Palaeovespa baltica* Cockerell	[19]	Cockerell 1909e
79.	Vespidae: *Polistes industrius* Théobald, Eumenidae: *Rhynchium*, sp.	[13]	Théobald 1937; Burnham 1978
80.	Eumenidae: *Alastor rottensis* Statz, Vespidae: *Vespa nigra* Statz	[8]	Statz 1936
81.	Formicidae	[55]	Hennig 1981
82.	Formicidae: *Cretacoformica explicata* Jell & Duncan	[53]	Jell & Duncan 1986

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
83.	Formicidae: *Peltopone petiolata* Dlussky	[39]	Dlussky 1975
84.	Formicidae: *Cretomyrma arnoldi* Dlussky	[37]	Dlussky 1975
85.	Formicidae: *Sphecomyrma freyi* Wilson, Carpenter & Brown	[36]	Wilson *et al.* 1967
86.	Formicidae: ?*Sphecomyrma* sp.	[35]	Burnham 1978
87.	Formicidae	[25]	Saunders *et al.* 1974
88.	Formicidae: Dolichoderinae	[24]	Lutz 1987
89.	Formicidae: *Polanskiella smekali* De Garcia	[20]	De Garcia 1983
90.	Formicidae: *Formica strangulata* Wheeler, and many other genera	[19]	Burnham 1978; Larsson 1978; Keilbach 1982
91.	Formicidae: *Oecophylla* sp.	[18]	Jarzembowski 1976
92.	Formicidae: *Archimyrmex rostratus* Cockerell	[15]	Carpenter 1930
93.	Formicidae: Aff. *Tapinoma*	[6]	Barthel & Hetzer 1982
94.	Formicidae: *Camponotus* sp.	[1]	Hopkins et al. 1971
95.	Sphecidae: *Archisphex crowsoni* Evans	[57]	Evans 1969
96.	Sphecidae: Aff. *Aphelotoma*	[54]	Jarzembowski 1984
97.	Sphecidae: Pemphredoninae	[53]	Jell & Duncan 1986
98.	Sphecidae: *Cretosphex incertus* Rasnitsyn	[52]	Rasnitsyn 1975
99.	Sphecidae: *Gallosphex cretaceus* Schlüter	[45]	Schlüter 1978
100.	Sphecidae: *Taimyrsphex pristinus* Evans	[37]	Evans 1973
101.	Sphecidae: *Lisponema singularis* Evans 1969	[35]	Evans 1969
102.	Sphecidae: *Crabo succinalis* Cockerell	[19]	Cockerell 1909e; Keilbach 1982
103.	Sphecidae	[8]	Bohart & Menke 1976
104.	Sphecidae: *Passaloecus munax* Sorg	[6]	Sorg 1986; Schumann & Wendt 1989
105.	Apidae: *Trigona prisca* Michener & Grimaldi	[36]	Michener & Grimaldi 1989a, 1989b
106.	Apidae: *Probombus hirsutus* Piton	[27]	Piton 1940; Burnham 1978
107.	Anthophoridae	[23]	Wilson 1978a
108.	Andrenidae: *Andrena wrisleyi* Salt, Melittidae: *Melitta willardi* Cockerell, Apidae: *Electrapis proava* (Menge)	[19]	Burnham 1978; Larsson 1978; Keilbach 1982
109.	Apidae: *Trigona dominicana* Wille & chandler	[17]	Burnham 1978
110.	Halictidae: *Halictus scudderiellus* Cockerell, Megachilidae: *Anthidium exhumatum* Cockerell, Anthophoridae: *Anthophora melfordi* Cockerell	[15]	Burnham 1978
111.	Apidae: *Trigona silacea* Wille	[11]	Burnham 1978
112.	Anthophoridae: *Xylocopa friesei* Statz	[8]	Burnham 1978
113.	Apidae: *Apis armbrusteri* Zeuner	[5]	Zeuner 1931
114.	Andrenidae: *Andrena primaeva* Cockerell, Halictidae: *Osmia antiqua* Heer	[3]	Burhnam 1978
115.	Mecoptera (Protomeropeidae): *Altajopanorpa brevis* Martynova	[97]	Martynova 1961; Hennig 1981
116.	Philopotamidae: *Prephilopotamus asiaticus*	[82]	Sukacheva 1973
117.	Eolepidopterygidae: *Eolepidopteryx jurassica* Rasnitsyn	[60]	Rasnitsyn 1983a; Whalley 1986
118.	Eolepidopterygidae: *Daiopteryx rasnitsyni* Skalski	[52]	Skalski 1984b; Whalley 1986
119.	Archaeolepidae: *Archaeolepis mane* Whalley	[69]	Whalley 1985, 1986
120.	Micropterygidae: *Parasabatinca aftimacrai* Whalley	[55]	Whalley 1977, 1986
121.	Micropterygidae: *Palaeosabatinca zherichini* Kozlov	[52]	Kozlov 1988b

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
122.	Micropterygidae	[45]	Schlüter 1978
123.	Micropterygidae: *Sabatinca proavitella* Rebel	[19]	Larsson 1978; Keilbach 1982
124.	Micropterygidae: *Micropteryx angelica* Jarzembowski	[18]	Jarzembowski 1980
125.	?Eriocraniidae: *Undopteryx sukatshevi* Skalski	[52]	Skalski 1979a; Whalley 1986
126.	?Lophocoronidae	[37]	Skalski 1979b
127.	Hepialiidae: *Prohepialus* sp.	[27]	Piton 1940
128.	Hepialiidae	[Priabon]	Harris 1984
129.	Hepialiidae: *Prohepialus* sp.	[18]	Jarzembowski 1980
130.	?Incurvariidae	[55]	Whalley 1977, 1986; Hennig 1981
131.	Nepticulidae: *Stigmellites*, leaf-mines	[39]	Kozlov 1988b
132.	"Mine type 3"	[29]	Crane & Jarzembowski 1980
133.	Tineidae: *Adela kuznetzovi* Kozlov	[19]	Kozlov 1988a
134.	Gracillariidae: *Bucculatrix platani* Kozlov, leaf-mine	[39]	Kozlov 1988a
135.	Macrolepidopteran egg	[Maestr]	Gall & Tiffney 1983; Whalley 1986
136.	Tineoidea	[35]	MacKay 1970; Whalley 1986
137.	Papilionoidea; Rhopalocera	[24,23]	Durden & Rose 1978; Lutz 1987
138.	Psychidae: ?*Sterrhopteryx pristinella* Rebel, Tineidae: *Proscardiites kusnezovi* Kozlov, Plutellidae: *Plutellites tenebricus* Kozlov, Lyonetiidae: *Prolyonetia cockerelli* Kusnezov, Tortricidae: *Tortricidiosis inclusa* Skalski, Oecophoridae: *Depressarites levipalpella* Rebel, Pyralidae: *Glendotrichia olgae* Kusnezov, Elachistidae: ?*Ambia cuprella*, Rebel	[19]	Rebel 1934, 1935; Kusnezov 1941; Skalski 1973b; Larsson 1978; Keilbach 1982; Kozlov 1987, 1988b
139.	Tineidae: *Copromorpha fossilis* Jarzembowski, ?Cossidae: *Gurnetia durranti* Cockerell, Pyralidae: *Pyralites preecei* Jarzembowski, Nymphalidae: *Nymphalites zeuneri* Jarzembowski, Lycaenidae: *Lithopsyche antiqua* Butler, Geometridae: *Geometridites larentiiformis* Jarzembowski	[18]	Jarzembowski 1980
140.	Lycaenidae: *Aquisextana irenai* The'obald, Libytheidae: *Prolibythea vagabunda* Scudder, Nymphalidae: *Apanthesis leuce* Scudder, Pieridae: *Oligodonta florissantensis* Brown	[15,13]	Scudder 1889; Théobald 1937; Brown 1976; Kozlov 1988b
141.	Nymphalidae: "Raupe mit Dornen," Pyralidae: "Kleine Raupe," Sphingidae: "Sphingidenraupe"	[7]	Zeuner 1931

MOUTHPART CLASS 14: FOSSATE COMPLEX
Fig. 70

1.	Mesoraphiididae: *Metaraphidia confusa* Whalley	[69]	Whalley 1985
2.	Permosialidae: *Permosialis sibirica* Martynova	[97]	Sharov 1953; Hennig 1981
3.	*Marquettia americana* (Cockerell)	[15]	Carpenter 1960
4.	*Actinophlebia intermixta* (Scudder)	[69]	Whalley 1988
5.	*Brongniartella*, sp.	[61]	Laurentiaux 1953

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
6.	Brongniartellidae	[57]	Jarzembowski 1984
7.	*Paractinophlebia curtsii* (Scudder)	[69]	Whalley 1988
8.	*Kalligramma flexuosum* Panfilov	[60]	Panfilov 1968
9.	Kalligrammatidae	[57]	Jarzembowski 1984
10.	Kalligrammatidae	[52]	Rasnitsyn 1988
11.	*Permithone belmontensis* Tillyard	[83]	Tillyard 1926d
12.	*Archaeosmylus costalis* Riek	[79]	Riek 1955
13.	*Archaeosmylus complexus* Whalley	[69]	Whalley 1988
14.	*Ascalaphus proavus* Hagen	[18]	Hagen 1855
15.	*Neadelphus protae* MacLeod	[19]	MacLeod 1970; Larsson 1978
16.	*Palaeoleon ferrogeneticus* Rice	[47]	Rice 1968
17.	*Dendroleon septemmontanus* Statz	[8]	Statz 1936
18.	*Mesonymphes hageni* Carpenter	[61]	Carpenter 1929; Lambkin 1988
19.	*Pronymphes mengeanus* Kröger	[19]	Kröger 1923; MacLeod 1970
20.	Nymphitidae	[60]	Rasnitsyn 1988
21.	Nymphitidae	[39]	Rasnitsyn 1988
22.	?*Triassopsychops superba* Tillyard	[74]	Tillyard 1922; Riek 1956
23.	*Beipiaopsychops triangulata* Hong	[64]	Hong 1983
24.	Psychopsidae	[57]	Whalley 1988
25.	*Propsychopsis helmi* Kröger	[19]	Kröger 1923; MacLeod 1970
26.	*Mesochrysopa zitteli* Meunier	[61]	Adams 1967
27.	*Mesopochrysa latipennis* Martynov	[60]	Adams 1967
28.	*Protopsychopsis venosa* Tillyard	[74]	Tillyard 1917b
29.	*Mesopolystoechus magnificus* Tillyard	[69]	Whalley 1988
30.	Prohemerobiidae	[60]	Rasnitsyn 1988
31.	Prohemerobiidae	[52]	Rasnitsyn 1988
32.	Chrysopidae	[45]	Schlüter 1978
33.	Chrysopidae	[19]	Larsson 1978
34.	Chrysopidae: Chrysopinae	[18]	Jarzembowski 1980
35.	Chrysopidae: Chrysopinae	[17]	Schlee & Glockner 1978
36.	*Archaeochrysa fracta* (Cockerell)	[15]	Adams 1967
37.	*Notochrysopa praeclava* Statz	[8]	Statz 1936
38.	*Prohemerobius*, sp.	[68]	Laurentiaux 1953
39.	*Prophlebonema resinata* Kröger	[19]	Kröger 1923; Larsson 1978
40.	*Hemerobius tinctus* Jarzembowski	[18]	Jarzembowski 1980
41.	Hemerobiidae	[15]	Wilson 1978a
42.	*Lithosmylidia lineata* Riek	[79]	Lambkin 1988
43.	*Mesopolystoechus magnificus* Tillyard	[69]	Whalley 1988
44.	*Mesopolystoechus wangyingziensis* Hong	[64]	Hong 1983
45.	*Promantispa relicta* (Cockerell)	[18]	Jarzembowski 1980
46.	*Banoberotha enigmatica* Whalley	[55]	Whalley 1980
47.	*Retinoberotha stuermeri* Schlüter	[45]	Schlüter 1978
48.	*Proberotha prisca* Kröger	[15]	Kröger 1923
49.	*Sogjuta speciosa* Martynov	[73]	Hennig 1981; Lambkin 1988
50.	*Mesosmylina exornata* Bode	[68]	Bode 1953; Lambkin 1988
51.	*Sinosmylites pectinatus* Hong	[64]	Hong 1983
52.	Osmylidae	[60]	Rasnitsyn 1988
53.	Osmylidae	[52]	Rasnitsyn 1988

(FOSSATE COMPLEX, continued)

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
54.	*Euporismites balli* Tillyard	[30]	Lambkin 1987
55.	*Protosmylus pictus* (Hagen)	[19]	Krüger 1923
56.	*Osmylidia requieta* (Scudder)	[15]	Carpenter 1943b
57.	Neurorthidae	[19]	Larsson 1978
58.	*Rhophalis relicta* Erichson	[19]	Krüger 1923; Keilbach 1982
59.	Sisyridae	[18]	Jarzembowski 1980
60.	Sisyridae	[6]	Schumann & Wendt 1989
61.	*Juraconiopteryx zherichini* Meinander	[60]	Meinander 1975
62.	*Glaesoconis fadiacra* Whalley	[55]	Whalley 1980
63.	*Glaesoconis cretica* Meinander	[37]	Meinander 1975
64.	*Hemisemidalis sharovi* Meinander	[19]	Meinander 1975

MOUTHPART CLASS 15: TUBULOMANDIBULATE

Fig. 73

1.	Trachypacheidae: *Sogdodromeus altus* Ponomarenko	[82]	Ponomarenko 1977b
2.	*Gyrinoides atavus* (Heer)	[72]	Hatch 1927
3.	Gryinidae	[Lias]	Dmitriev & Zherikin 1988
4.	*Angarogyrus minimus* Ponomarenko	[60]	Ponomarenko 1977b; Crowson *et al.* 1967
5.	Gyrinidae	[53]	Jell & Duncan 1986
6.	*Avitortor primitivus* Ponomarenko	[52]	Ponomarenko 1977b
7.	*Gyrinoides limbatus* Motschulsky	[19]	Hatch 1927; Larsson 1978
8.	*Dineutes insignis* Heer	[3]	Heer 1862; Hatch 1927
9.	Haliplidae	[52]	Dmitriev & Zherikin 1988
10.	?*Angaragabus jurassicus* Ponomarenko	[67]	Ponomarenko 1963
11.	*Liadytes crassus* Ponomarenko	[52]	Ponomarenko 1977b; Crowson 1981
12.	Noteridae	[Paleoc.]	Dmitriev & Zherikin 1988
13.	*Necronectes latus* Ponomarenko	[71]	Ponomarenko 1977b
14.	*Necronectes aquaticus* Ponomarenko	[67]	Ponomarenko 1977b
15.	*Stygeonectes jurassicus* Ponomarenko	[66]	Ponomarenko 1977b
16.	*Charnoscapha ovata* Ponomarenko	[60]	Ponomarenko 1977b
17.	Coptoclavidae	[52]	Dmitriev & Zherikin 1988
18.	*Actea sphinx* Germar	[61]	Ponomarenko 1971
19.	*Cretodytes latipes* Ponomarenko	[52]	Ponomarenko 1977b
20.	Dytiscidae	[53]	Jell & Duncan 1986
21.	Dytiscidae	[33]	George 1952
22.	*Hyphydrus*, sp.	[19]	Keilbach 1982
23.	*Hydroporus sedimentorum* Wickham	[15]	Wickham 1914
24.	*Palaeogyrinus*	[8]	Darlington 1929
25.	*Schistomerus califorense* Palmer	[4]	Palmer 1957
26.	*Aff. Agabus* sp.	[2]	Schawaller 1986
27.	Dytiscidae	[1]	Hopkins *et al.* 1971
28.	*Parahygrobia natans* Ponomarenko	[62]	Ponomarenko 1977b
29.	?Elateridae	[72]	Heer 1865
30.	Elateridae	[69]	Whalley 1985
31.	*Luciola* sp.	[19]	Larsson 1978
32.	*Chauliognathus pristinus* Scudder	[15]	Scudder 1900; Wickham 1913,1914

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
33.	*Pseudoplatypterus scheelei* Kleine	[19]	Keilbach 1982
34.	Cantharidae	[53]	Jell & Duncan 1986
35.	*Calomorphocerus cerambyx* Schaufuss	[19]	Larsson 1978; Keilbach 1982
36.	*Silis chiapasensis* Wittmer	[11]	Wittmer 1963
37.	*Malthodes* sp.	[6]	Schumann & Wendt 1989
38.	*Cantharis* sp.	[2]	Schawaller 1986

CLASS 16: MOUTHHOOK

Fig. 76

1.	Bibionidae	[76]	Olsen *et al.* 1978
2.	Mycetophilidae: *Prodocidia spectra* Whalley	[69]	Whalley 1985
3.	Cecidomyiidae	[55]	Schlee & Dietrich 1970; Gagné 1977
4.	Cecidomyiidae	[37]	Zherikin & Sukacheva 1973
5.	Cecidomyiidae: *Cretocatocha mcalpinei* Gagné	[35]	Gagné 1977
6.	Cecidomyiidae	[23]	Wilson 1978a
7.	Cecidomyiidae: *Cecidomyia conjuncta* Meunier	[19]	Meunier 1899; Keilbach 1982
8.	Cecidomyiidae	[17]	Schlee & Glockner 1978
9.	Cecidomyiidae	[15]	Wilson 1978a
10.	Cecidomyiidae: *Clinodiplosis* aff. *terrestris* (Felt)	[11]	Gagné 1973
11.	Cecidomyiidae	[8]	Statz 1944c
12.	Cecidomyiidae	[6]	Schumann & Wendt 1989
13.	Rhagionidae: *Protobrachyceron liasinum* Handlirsch	[68]	Kalugina & Kovalev 1985
14.	Rhagionidae: *Palaeobrachyceron hennigi* Kovalev	[67]	Kovalev 1981
15.	Xylomyiidae: *Mesozolva parva* Hong	[64]	Hong 1983
16.	Rhagionidae: *Palaeoptiolina scobloi* Kovalev	[62]	Kovalev 1982
17.	Rhagionidae: *Probolbomyia modesta* Ussatchov, Acroceridae: *Archocyrtus gibbosus* Ussatchov, Nemestrinidae: *Archinemestrinus karatavicus* Rohdendorf	[60]	Ussatchov 1968; Rohdendorf 1968b
18.	Stratiomyiidae: "dipterous larva, species 1"	[56]	Whalley & Jarzembowski 1985
19.	Rhagionidae	[57]	Jarzembowski 1984
20.	Rhagionidae: *Atherimorpha festuca* Jell & Duncan	[53]	Jell & Duncan 1986
21.	Rhagionidae	[37]	Zherikin & Sukacheva 1973
22.	Stratiomyiidae: *Cretaceogaster pygmaeus* Teskey	[35]	Teskey 1971
23.	Tabanidae	[24]	Lutz 1987
24.	Stratiomyiidae, Acroceridae, ?Tabanidae	[23]	Wilson 1978a
25.	Stratiomyiidae	[20]	De Garcia 1983
26.	Xylomyiidae: *Solva nana* (Loew)	[19]	Loew 1850; Hennig 1967a
27.	Stratiomyiidae	[18]	Jarzembowski 1976
28.	Tabanidae	[17]	Schlee & Glockner 1978
29.	Rhagionidae, Stratiomyiidae, Nemestriniidae, Tabanidae; Rhagionidae: *Rhagio primaevus* Théobald	[15,13]	Théobald 1937; Wilson 1978a
30.	Stratiomyiidae: *Pachygaster antiqua* James	[11]	James 1971
31.	Stratiomyiidae	[9]	Zeuner 1938
32.	Rhagionidae	[6]	Schumann & Wendt 1989
33.	Bombyliidae: *Palaeoplatypygus zaitzevi* Kovalev	[65]	Kovalev 1985

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
34.	Protomphralidae: *Protomphrale martynovi* Rohdendorf	[60]	Rohdendorf 1974
35.	Bombyliidae	[37]	Zaitzev 1981
36.	Asilidae	[23]	Wilson 1978a; Grande 1980
37.	Therevidae: *Glaesorthactia magnicornis* Meunier, Asilidae: *Asilus klebsi* Meunier	[19]	Meunier 1908a,1909; Hennig 1967c
38.	Bombyliidae: *Glabellula kuehnei* Schlüter	[17]	Schlüter 1976
39.	Therevidae, Asilidae, Mydidae, Bombyliidae; Asilidae: *Machimus kollmanni* Timon-David, Bombyliidae: *Praecytherea sardi* Théobald	[15,14] 13]	Théobald 1937; Timon-David 1943; Wilson 1978a
40.	Asilidae: *Protoloewinella kielbachi* Schumann, Bombyliidae	[6]	Schumann 1984; Schumann & Wendt 1989
41.	Empididae: *Protempis antennata* Ussatchov	[60]	Ussatchov 1968
42.	Empididae	[57]	Jarzembowski 1984
43.	Empididae: *Trichinites cretaceus* Hennig	[55]	Hennig 1970
44.	Empididae: *Ecommocydromia difficilis* Schlüter	[45]	Schlüter 1978
45.	Empididae: *Empis orapaensis* Waters	[43]	Waters 1989a
46.	Empididae: *Cretoplatypalpus archaeus* Kovalev	[42]	Kovalev 1978
47.	Empididae	[40]	Langenheim *et al.* 1960
48.	Empididae: *Archiplatypalpus cretaceus* Kovalev, Dolichopodidae: *Retinitus nervosus* Negrobov	[37]	Kovalev 1974; Negrobov 1978
49.	Empididae: ?Microphorinae	[35]	Hennig 1970
50.	Empididae	[32]	Wilson 1978a
51.	Dolichopodidae, Empididae	[24]	Wilson 1978a
52.	Empididae: *Rhamphomyia porrecta* Meunier, Dolichopodidae: *Xiphandrium splendidum* Meunier	[19]	Meunier 1907, 1908b; Keilbach 1982
53.	Dolichopodidae	[18]	Jarzembowski 1976
54.	Dolichopodidae	[17]	Schlee & Glockner 1978
55.	Empididae: *Tachydromia theobaldi* Timon-David; Empididae	[15,14]	Timon-David 1943; Wilson 1978a
56.	Dolichopodidae, Empididae	[6]	Schumann & Wendt 1989
57.	Platypezidae, Sciadoceridae	[55]	Kovalev 1985
58.	Sciadoceridae, Platypezidae	[37]	Zherikin & Sukacheva 1973
59.	Phoridae: *Metopina goeleti* Grimaldi	[36]	Grimaldi 1989
60.	Ironomyiidae: *Cretonomyia pristina* McAlpine, Sciadoceridae: *Sciadophora bostoni* McAlpine & Martin	[35]	McAlpine & Martin 1966; McAlpine 1973
61.	Platypezidae	[23]	Wilson 1978a
62.	Sciadoceridae: *Archiphora robusta* (Meunier)	[19]	Meunier 1905; Hennig 1964
63.	Phoridae: *Metopina* sp.	[17]	Grimaldi *et al.* 1989
64.	Platypezidae, Phoridae	[15]	Wilson 1978a
65.	Phoridae: *Bohrniphora poinari* Disney	[11]	Disney 1987
66.	Phoridae	[6]	Schumann & Wendt 1989
67.	Syrphidae	[37]	Kovalev 1985
68.	?Pipunculidae	[35]	McAlpine & Martin 1969
69.	Syrphidae	[32]	Wilson 1978a
70.	Syrphidae	[23]	Wilson 1978a
71.	Syrphidae: *Pseudosphegina carpenteri* Hull	[19]	Hull 1957
72.	Syrphidae; Syrphidae: *Chilosia padovana* Timon-David	[15,14]	Timon-David 1943; Wilson 1978a

(MOUTHHOOK, continued)

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
73.	Syrphidae: *Platycheirus persistens* Hull	[10]	Hull 1938
74.	Syrphidae: *Syrphopsis globosiceps* Zeuner; Syrphidae	[7,6]	Zeuner 1931; Schumann & Wendt 1989
75.	Conopidae	[55]	Hennig 1971b
76.	Conopidae	[23]	Wilson 1978a
77.	Conopidae: *Palaeomyopa tertiaria* Meunier	[19]	Meunier 1912; Keilbach 1982
78.	Tephritidae, Piophilidae	[23]	Wilson 1978a
79.	Pallopteridae: *Pallopterites electrica* Hennig, Lonchaeidae: *Morgea mcalpinei* Hennig	[19]	Hennig 1967b
80.	Otitidae, Tephritidae, Piophilidae	[15]	Wilson 1978a
81.	Megamerinidae: *Palaeotanypeza spinosa* Meunier, Micropezidae: *Electrobata* sp.	[19]	Hennig 1965, 1969
82.	Diopsidae: *Prosphyracephala succini* Loew, Psilidae: *Electrochyliza succini* Hennig	[19]	Hennig 1965, 1969
83.	Diopsidae: *Aff. Prosphyracephala* or *Sphyracephala*	[13]	Lutz 1985a
84.	Diopsidae: *Prosphyacephala rubiensis* Lewis	[Chattian]	Lewis 1971a
85.	Diopsidae	[6]	Schumann & Wendt 1989
86.	Lauxaniidae: "*Lonchaea*" *senescens* Scudder	[32]	Cockerell 1909a
87.	Sciomyzidae, Sepsidae, Lauxaniidae	[23]	Wilson 1978a
88.	Sciomyzidae: *Prophaeomyia loewi* Hennig	[19]	Hennig 1965
89.	Sciomyzidae, Sepsidae	[15]	Wilson 1978a
90.	Clusiidae: *Electroclusoides meunieri* (Hendel)	[19]	Hennig 1969
91.	Anthomyzidae: *Xenanthomyza larssoni* Hennig, Asteiidae: *Succiniasteia carpenteri* Hennig	[19]	Hennig 1967b, 1969
92.	Periscelidae: *Periscelis annectans* Sturtevant	[11]	Sturtevant 1963
93.	?Heleomyzidae	[23]	Wilson 1978a
94.	Cryptochaetidae: *Phanerochaetum tuxeni* Hennig	[19]	Hennig 1969
95.	Agromyzidae, Heleomyzidae, Lauxaniidae, Heleomyzidae: *Helomyza fagei* Timon-David	[15,14]	Timon-David 1943; Wilson 1978a
96.	?Chloropidae	[35]	Kovalev 1985
97.	Chloropidae: *Protoscinella electrica* Hennig, Carnidae: *Neoneurites enigmatica* Hennig	[19]	Hennig 1969, 1972a
98.	Chloropidae: *Hippelates brodiei* Cockerell	[18]	Cockerell 1916b
99.	?Milichiidae	[36]	Grimaldi *et al.* 1989
100.	Diastatidae: *Pareuthychaeta electrica* Hennig, Milichiidae: "*Phyllomyza*" Jaegeri Hennig	[19]	Hennig 1967b, 1971b
101.	Drosophilidae: *Chymomyza primaeva* Grimaldi	[17]	Grimaldi 1987
102.	Drosophilidae: *Neotanygastrella wheeleri* Grimaldi	[11]	Grimaldi 1987
103.	Calliphoridae: *Cretaphormia fowleri* McAlpine	[35]	McAlpine 1970
104.	Oestridae	[32]	Wilson 1978a
105.	Muscidae, Tachinidae, Oestridae, Glossinidae, Anthomyiidae	[23]	Wilson 1978a
106.	Muscidae: *Fannia scalaris* Fabricius, Tachinidae: *Tachina* sp.	[19]	Keilbach 1982
107.	Anthomyiidae, Glossinidae, Muscidae, Tachinidae, Oestridae	[15]	Wilson 1978a
108.	Hippoboscidae: *Ornithomya rottensis* (Statz)	[8]	Maa 1966

MOUTHPART CLASS 17: HAUSTORIATE

Fig. 79

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
1.	Archaeolepidae: *Archaeolepis mane* Whalley	[69]	Whalley 1985, 1986
2.	*Electralberta cretacica* Botosaneanu & Wichard	[35]	Botosaneanu & Wichard 1983
3.	Psychomyiidae	[34]	Wolbert *et al.* 1988
4.	*Archaeotinodes lanceolata* Ulmer	[19]	Keilbach 1982
5.	*Hydropsyche submaculata* Kolenati	[19]	Keilbach 1982
6.	*Leptonema* sp.	[17]	Wichard 1987
7.	Hydropsychidae	[15]	Wilson 1978a
8.	*Archaeopolycentra zherikhini* Botosaneanu & Wichard	[37]	Botosaneanu & Wichard 1983
9.	*Antillopsyche* sp.	[17]	Wichard 1987
10.	*Prephilopotamus asiaticus* Sukacheva	[82]	Sukacheva 1973
11.	Philopotamidae	[37]	Botosaneanu & Wichard 1983
12.	*Chimarra succini* Wichard	[17]	Wichard 1983
13.	*Necrotaulius proximus* Sukacheva	[70]	Sukacheva 1973
14.	*Necrotaulius marginatus* Bode	[68]	Bode 1953
15.	*Necrotaulius fascialatus* Hong	[64[	Hong 1983
16.	*Karataulius aeternus* Sukacheva	[60]	Sukacheva 1968b
17.	Rhyacophilidae	[L. Jura]	Dmitriev & Zherikin 1988
18.	*Rhyacophila antiquissima* Botosaneanu & Wichard	[37]	Botosaneanu & Wichard 1983
19.	*Rhyacophila kutscheri* Mey	[19]	Mey 1988
20.	Glossosomatidae	[19]	Dmitriev & Zherikin 1988
21.	*Campsiophora* sp.	[17]	Wichard 1987
22.	*Palaeohydrobiosis siberambra* (Botosaneanu & Wichard	[37]	Botosaneanu & Wichard 1982
23.	Hydroptilidae	[37]	Dmitriev & Zherikin 1988
24.	Hydroptilidae	[23]	Wilson 1978a
25.	*Agraylea spathifera* Ulmer	[19]	Larsson 1978; Keilbach 1982
26.	*Alisotrichia* sp.	[17]	Wichard 1987
27.	Hydroptilidae	[15]	Wilson 1978a
28.	*Prorhyacophila furcata* Sukacheva	[70]	Sukacheva 1973
29.	*Dysoneura trifurcata* Sukacheva	[60]	Sukacheva 1968b
30.	*Baissophryganoides monstruosus* Sukacheva	[52]	Sukacheva 1968a
31.	Phryganeidae	[15]	Wilson 1978a
32.	*Phryganea lavrushini* Cockerell	[12]	Cockerell 1925a
33.	*Baissoferus latus* Sukacheva	[52]	Sukacheva 1968a
34.	Lepidosomatidae	[19]	Dmitriev & Zherikin 1988
35.	Limnephilidae	[15]	Wilson 1978a
36.	*Limnephilus recultus* Cockerell	[12]	Cockerell 1925a
37.	*Goera gracilicornis* Ulmer	[19]	Keilbach 1982
38.	*Brachycentrus labialis* Hagen	[19]	Pictet-Baraban & Hagen 1856; Keilbach 1982
39.	Vitimotaulidae	[60]	Rasnitsyn 1988
40.	*Vitimotaulius legibilis* Sukacheva	[52]	Sukacheva 1968a
41.	*Beraeodes pectinata* Ulmer	[19]	Keilbach 1982
42.	Sericostomatidae	[37]	Zherikin & Sukacheva 1973
43.	*Arachaeocrunoecia valdicornis* Ulmer	[19]	Keilbach 1982

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
44.	Sericostomatidae	[15]	Wilson 1978a
45.	Odontoceridae	[15]	Wilson 1978a
46.	*Molanna crassicornis* Ulmer	[19]	Larsson 1978; Keilbach 1982
47.	Helicopsychidae	[19]	Dmitriev & Zherikin 1988
48.	*Helicopsyche* sp.	[17]	Wichard 1987
49.	?*Oecetis* sp.	[53]	Jell & Duncan 1986
50.	*Praeathripsodes jantar* Botosaneanu & Wichard	[37]	Botosaneanu & Wichard 1983
51.	*Nectopsyche* sp.	[17]	Wichard 1983
52.	Leptoceridae	[15]	Wilson 1978a
53.	Calamoceratidae	[53]	Jell & Duncan 1986
54.	*Rhabdoceras fusculus* Ulmer	[19]	Larsson 1978; Keilbach 1982

MOUTHPART CLASS 18: LABELLATE

Fig. 82

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
1.	Unnamed family: *Tarwinia australis* Jell & Duncan	[53]	Jell & Duncan 1986
2.	*Cyclochorista convexicosta* Martynova	[97]	Martynova 1958, 1961
3.	*Permochorista australica* Tillyard	[83]	Tillyard 1926b
4.	*Afristella delicatula* Riek	[78]	Riek 1974
5.	*Mesopanorpa umbrata* Martynov	[71]	Martynov 1937a
6.	*Mesopanorpa luanpingensis* Hong	[64]	Hong 1983
7.	*Mesopanorpa* sp.	[57]	Jarzembowski 1984
8.	*Prochoristella leongatha* Jell & Duncan	[53]	Jell & Duncan 1986
9.	Protomeropeidae: *Altajopanorpa pilosa* Martynova	[97]	Martynova 1959
10.	Dictyodipteridae: *Dictyodiptera multinervis* Rohdendorf	[73]	Rohdendorf 1961, 1974
11.	Tipulidae	[76]	Olsen et *al.* 1978
12.	Tipulidae: *Tipuloidea rhaetica* Wieland	[Norian]	Wieland 1925
13.	Tipulidae: *Dictyotipula densa* Rohdendorf	[73]	Rohdendorf 1962, 1974
14.	Tipulidae: *Architipula simplex* Handlirsch	[68]	Handlirsch 1939
15.	Trichoceridae: *Eotrichcera christinae* Kalugina	[66]	Kalugina & Kovalev 1985
16.	Tipulidae: *Eotipulina fumosa* Kalugina	[65]	Kalugina & Kovalev 1985
17.	Tipulidae: *Sinotipula huabeinensis* Hong	[64]	Hong 1983
18.	Trichoceridae: *Mailotrichocera jurassica* Kalugina	[62]	Kalugina & Kovalev 1985
19.	Tipulidae: Limoniinae	[60]	Rasnitsyn 1988
20.	Tipulidae: *Corethrium pertinax* Westwood	[59]	Westwood 1854; Rohdendorf 1974
21.	Tipulidae: Aff. *Gynoplistia*	[57]	Jarzembowski 1984
22.	Tipulidae: Lomoniinae	[53]	Jell & Duncan 1986
23.	Trichoceridae	[52]	Rasnitsyn 1988
24.	Tipulidae: Limoniinae	[42]	Rasnitsyn 1988
25.	Tipulidae	[37]	Zherikin & Sukacheva 1973
26.	Tipulidae: *Limnophila* sp.	[32]	Mitchell & Wighton 1979
27.	Tipulidae	[24,23]	Wilson 1978a; Lutz 1987
28.	Trichoceridae: *Oligotrichocera antiqua* Keilbach	[19]	Keilbach 1982
29.	Tipulidae: *Tipula limiformis* Cockerell	[18]	Cockerell 1916b
30.	Tipulidae	[17]	Schlee & Glockner 1978
31.	Tipulidae: *Tipula wilmatteae* Melander	[15]	Melander 1949

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
32.	Tipulidae; Tipulidae: *Tipula carpenteri* Alexander	[11,10]	Alexander 1938; Alexander & Byers 1981
33.	Trichoceridae: *Trichocera* sp.	[6]	Schumann & Wendt 1989
34.	Trichoceridae: *Trichocera* sp.	[6]	Schumann & Wendt 1989
35.	Blepharoceridae	[42]	Rasnitsyn 1988
36.	*Praemacrochile stackelbergi* Kalugina	[66]	Kalugina & Kovalev 1985
37.	Tanyderidae	[60]	Rasnitsyn 1988
38.	*Macrochile spectrum* Loew	[19]	Loew 1851; Crampton 1926
39.	*Eolimnobia geinitzi* Handlirsch	[68]	Handlirsch 1908; Rohdendorf 1974
40.	Eoptychopteridae:	[60]	Rasnitsyn 1988
41.	*Bolboia mira* Kalugina	[58]	Kalugina 1989
42.	Eoptychopteridae	[52]	Rasnitsyn 1988
43.	*Ptychoptera mesozoica* Kalugina	[52]	Kalugina 1989
44.	Ptychopteridae	[32]	Wilson 1978a
45.	*Bittacomorphella miocaenica*	[15]	Alexander 1981c
46.	*Ptychoptera deleta* Novak	[8]	Alexander 1981c
47.	Psychodidae: *Mesopsychoda dasyptera* Brauer, Redtenbacher & Ganglbauer	[67]	Brauer *et al.* 1889
48.	Chironomidae: *Architendipes tschernovskii* Rohdendorf	[73]	Rohdendorf 1974
49.	Paraxmyiidae	[Lias]	Dmitriev & Zherikin 1988
50.	*Protolbiogaster rhaetica* Rohdendorf	[73]	Rohdendorf 1974
51.	*Protoplecia liasina* (Geinitz)	[68]	Geinitz 1884; Peterson 1975
52.	*Archipleciomima longicornis*	[66]	Kalugina & Kovalev 1985
53.	*Mesoplecia jurassica* Rohdendorf	[60]	Rohdendorf 1938
54.	*Simulidium priscum* Westwood	[59]	Westwood 1854; Rohdendorf 1974
55.	Protopleciidae	[52]	Dmitriev & Zherikin 1988
56.	Bibionidae	[76]	Olsen *et al.* 1978
57.	?Bibionidae: *Beipiaoplecia malleformis* Lin	[64]	Lin 1976
58.	Bibionidae	[52]	Rasnitsyn 1988
59.	Bibionidae	[43]	Rayner 1987
60.	?Bibionidae	[37]	Zherikin & Sukacheva 1973
61.	Bibionidae	[35]	McAlpine & Martin 1969
62.	Bibionidae	[32]	Wilson 1978a
63.	Bibionidae	[23]	Wilson 1978a
64.	*Plecia crassicornis* Loew	[19]	Loew 1850; Keilbach 1982
65.	*Bibiodites confluens* Cockerell	[18]	Cockerell 1916b
66.	*Hesperinus immutabilis* Melander; *Bibio spectabilis* Théobald	[15,13]	Théobald 1937; Melander 1949
67.	*Plecia amagua* Cockerell; *Plecia pristina* Hardy	[12,11]	Cockerell 1925a; Hardy 1971
68.	*Bibio sticheli* Handlirsch	[9]	Handlirsch 1908; Zeuner 1938
69.	*Rhaetofungivora reticulata* Rohdendorf	[73]	Rohdendorf 1962
70.	*Rohdendorfomyiella incorporalis* Kovalev	[66]	Kalugina & Kovalev 1985
71.	*Bryanka elegantissima* Kovalev	[65]	Kalugina & Kovalev 1985
72.	*Willihennigia curtipes* Kovalev	[62]	Kalugina & Kovalev 1985
73.	Pleciofungivoridae	[60]	Rasnitsyn 1988
74.	Pleciofungivoridae	[52]	Rasnitsyn 1988
75.	Hyperoscleidae: *Prohyperoscelis jurassicus* Kovalev	[65]	Kalugina & Kovalev 1985
76.	*Prodocidia spectra* Whalley	[69]	Whalley 1985

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
77.	Sciophilinae	[57]	Whalley 1985
78.	*Pseudalysiinia fragmenta* Jell & Duncan	[53]	Jell & Duncan 1986
79.	Mycetophilidae	[52]	Rasnitsyn 1988
80.	*Schlueterimyia cenomanica* Matile	[45]	Matile 1981
81.	Mycetophilidae	[42]	Rasnitsyn 1988
82.	Mycetophilidae	[37]	Zherikin & Sukacheva 1973
83.	Mycetophilidae	[36]	Grimaldi *et al.* 1989
84.	Sciophilinae	[35]	McAlpine & Martin 1969
85.	Mycetophilidae	[32]	Wilson 1978a
86.	Mycetophilidae	[23]	Wilson 1978a
87.	*Mycetophila antennata* (Loew)	[19]	Loew 1850; Keilbach 1982
88.	*Mycetophila vectensis* Cockerell	[18]	Cockerell 1916b
89.	*Proceroplatus hennigi* Schmalfuss	[17]	Schmalfuss 1979; Keilbach 1982
90.	*Exechia priscula* Melander	[15]	Melander 1949
91.	Mycetophilidae	[8]	Statz 1944a
92.	Mycetophilidae	[6]	Schumann & Wendt 1989
93.	Sciaridae	[55]	Grimaldi *et al.* 1989
94.	Sciaridae	[52]	Rasnitsyn 1988
95.	Sciaridae	[42]	Rasnitsyn 1988
96.	*Sciara* cf. *deflectuosa* Meunier	[36]	Grimaldi *et al.* 1989
97.	Sciaridae	[37]	McAlpine & Martin 1969
98.	Sciaridae	[32]	Wilson 1978a
99.	*Sciara* sp.	[23]	Wilson 1978a
100.	*Heterotricha hirta* (Loew)	[19]	Loew 1850; Keilbach 1982
101.	*Sciara gurnetensis* Cockerell	[18]	Cockerell 1916b
102.	Sciaridae	[17]	Baroni-Urbani & Saunders 1982
103.	*Sciara sopora* Melander; *Sciara* sp.	[15,13]	Théobald 1937; Melander 1949
104.	*Sciara weylandi* Statz	[8]	Statz 1944c
105.	Sciaridae	[6]	Schumann & Wendt 1989
106.	Cecidomyiidae	[55]	Schlee & Dietrich 1970; Gagné 1973
107.	Cecidomyiidae	[37]	Zherikin & Sukacheva
108.	*Cretocatocha mcalpinei* Gagné	[35]	Gagné 1977
109.	Cecidomyiidae	[23]	Wilson 1978a; Grande 1980
110.	*Cecidomyia conjuncta* Meunier	[19]	Meunier 1899b; Keilbach 1982
111.	Cecidomyiidae	[17]	Schlee & Glockner 1978
112.	Cecidomyiidae	[15]	Wilson 1978a
113.	*Clinodiplosis* aff. *terrestris* (Felt)	[11]	Gagné 1973
114.	Cecidomyiidae	[8]	Statz 1944a
115.	Cecidomyiidae	[6]	Schumann & Wendt 1989
116.	Xylophagidae	[42]	Rasnitsyn 1988
117.	*Xylophagus eridanus* Meunier	[19]	Meunier 1909; Keilbach 1982
118.	Stratiomyiidae: "dipterous larva, species 1"	[56]	Whalley & Jarzembowski 1985
119.	*Cretogaster pygmaeus* Teskey	[35]	Teskey 1971
120.	Stratiomyiidae	[23]	Wilson 1978a; Grande 1980
121.	Stratiomyiidae	[20]	De Garcia 1983
122.	*Rhacicerus formosus* (Loew)	[19]	Loew 1850; Keilbach 1982
123.	Stratiomyiidae	[18]	Jarzembowski 1976
124.	Stratiomyiidae	[15]	Wilson 1987a

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
125.	*Pachygaster antiqua* James	[11]	James 1971
126.	Stratiomyiidae	[9]	Zeuner 1938
127.	*Archocyrtus gibbosus* Ussatchov	[60]	Ussatchov 1968
128.	?*Protohirmoneura jurassica* Handlirsch	[61]	Handlirsch 1906
129.	*Archinemestrinus karatavicus* Rohdendorf	[60]	Rohdendorf 1968b
130.	Nemestriniidae	[52]	Rasnitsyn 1988
131.	*Hirmoneura willistoni* (Cockerell)	[15]	Cockerell 1910; Bequaert & Carpenter 1936
132.	*Nemestrina reticulata* Latreille	[13]	Bequaert & Carpenter 1936
133.	Tabanidae	[24]	Lutz 1987
134.	?Athericidae	[24]	Lutz 1987
135.	*Protobrachyceron liasinum* Handlirsch	[68]	Handlirsch 1908
136.	Bombyliidae: *Palaeoplatypygus zaitzevi* Kovalev	[65]	Kalugina & Kovalev 1985
137.	*Protempis antennata* Ussatchov	[60]	Ussatchov 1968
138.	Dolichopodidae	[37]	Dmitriev & Zherikin 1988
139.	Dolichopodidae	[23]	Wilson 1978a
140.	*Xiphandrium splendidum* Meunier	[19]	Meunier 1907; Keilbach 1982
141.	Dolichopodidae	[18]	Jarzembowski 1976
142.	Dolichopodidae	[17]	Schlee & Glockner 1978
143.	*Sciopus combaluzieri* Timon-David	[14]	Timon-David 1943
144.	Dolichopodidae	[6]	Schumann & Wendt 1989
145.	Platypezidae, Sciadoceridae	[55]	Kovalev 1985
146.	Sciadoceridae, Platypezidae	[37]	Zherikin & Sukacheva 1973
147.	Phoridae: *Metopina goeleti* Grimaldi	[36]	Grimaldi 1989
148.	Sciadoceridae: *Sciadophora bostoni* McAlpine & Martin	[35]	McAlpine & Martin 1966
149.	Platypezidae	[23]	Wilson 1978a; Grande 1980
150.	Sciadoceridae: *Archiphora robusta* Meunier	[19]	Meunier 1905b; Hennig 1964
151.	Phoridae: *Metopina* sp.	[17]	Grimaldi 1989
152.	Platypezidae, Phoridae	[15]	Wilson 1978a
153.	Phoridae: *Dohrniphora poinari* Disney	[11]	Disney 1987
154.	Phoridae	[6]	Schumann & Wendt 1989
155.	Syrphidae	[37]	Kovalev 1985
156.	?Pipunculidae	[37]	McAlpine & Martin 1969
157.	Syrphidae	[32]	Wilson 1978a
158.	Syrphidae	[23]	Wilson 1978a; Grande 1980
159.	Syrphidae: *Pseudosphegina carpenteri* Hull	[19]	Hull 1957
160.	Syrphidae: *Chilosia padovana* Timon-David	[14]	Timon-David 1943
161.	Syrphidae: *Platycheirus persistens* Hull	[10]	Hull 1938
162.	Syrphidae: *Syrphopsis globosiceps* Zeuner; Syrphidae	[7,6]	Zeuner 1931; Schumann & Wendt 1989
163.	Conopidae	[55]	Hennig 1971a
164.	Conopidae	[23]	Wilson 1978a; Grande 1980
165.	Conopidae: *Palaeomyopa tertiaria* Meunier	[19]	Meunier 1912; Keilbach 1982
166.	Tephritidae, Piophilidae	[23]	Wilson 1978a; Grande 1980
167.	Pallopteridae: *Pallopterites electrica* Hennig, Lonchaeidae: *Morgea mcalpinei* Hennig	[19]	Hennig 1967b, 1969
168.	Otitidae, Tephritidae, Piophilidae	[15]	Wilson 1978a

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
169.	Megamerinidae: *Palaeotanypeza spinosa* Meunier, Micropezidae: *Electrobata* sp.	[19]	Hennig 1965, 1969
170.	Diopsidae: *Prosphyracephala succini* Loew, Psilidae: *Electrochyliza succini* Hennig	[19]	Hennig 1965, 1969
171.	Diopsidae: Aff. *Prosphyracephala* or *Sphyracephala*	[13]	Lutz 1985a
172.	Diopsidae: *Prosphyracephala rubiensis* Lewis	[Chattian]	Lewis 1971
173.	Diopsidae	[6]	Schumann & Wendt 1989
174.	Lauxaniidae: "*Lochaea*" *senescens* Scudder	[32]	Cockerell 1909a
175.	Sciomyzidae, Sepsidae, Lauxaniidae	[23]	Wilson 1978a; Grande 1980
176.	Sciomyzidae: *Prophaeomyia loewi* Hennig	[19]	Hennig 1965
177.	Sepsidae, Sciomyzidae	[15]	Wilson 1978a
178.	Clusiidae: *Electroclusoides meunieri* (Hendel)	[19]	Hennig 1969
179.	Anthomyzidae: *Xenanthomyza larssoni* Hennig, Asteidae: *Succiniasteia carpenteri* Hennig	[19]	Hennig 1967b, 1969
180.	Periscelidae: *Periscelis annectans* Sturtevant	[11]	Sturtevant 1963
181.	Heleomyzidae	[23]	Wilson 1978a; Grande 1980
182.	Cryptochaetidae: *Phanerochaetum tuxeni* Hennig	[19]	Hennig 1969
183.	Agromyzidae, Heleomyzidae, Lauxaniidae	[15]	Wilson 1978a
184.	?Chloropidae	[35]	Kovalev 1985
185.	Chloropidae: *Protoscinella electrica* Hennig, Carnidae: *Neoneurites enigmatica* Hennig	[19]	Hennig 1969, 1972a
186.	Chloropidae: *Hippelates brodiei* Cockerell	[18]	Cockerell 1916b
187.	?Milichiidae	[36]	Grimaldi *et al.* 1989
188.	Diastatidae: *Pareuthychaeta electrica* Hennig, Milichiidae: "*Phyllomyza*" *jaegeri* Hennig	[19]	Hennig 1967, 1971b
189.	Drosophilidae: *Chymomyza primaeva* Grimaldi	[17]	Grimaldi 1987
190.	Drosophilidae: *Phyllomyza hurdi* Sabroski	[11]	Sabroski 1963
191.	Calliphoridae: *Cretaphormia fowleri* McAlpine	[35]	McAlpine 1970
192.	Oestridae	[32]	Wilson 1978a
193.	Muscidae, Oestridae, Anthomyiidae	[23]	Wilson 1978a; Grande 1980
194.	Muscidae: *Fannia scalaris* Fabricius	[19]	Keilbach 1982
195.	Anthomyiidae, Muscidae, Oestridae	[15]	Wilson 1978a
196.	Glossinidae	[23]	Wilson 1978a; Grande 1980

MOUTHPART CLASS 19: SIPHONATE

Fig. 85

1.	Philopotamidae: *Prophilopotamus asiaticus* Sukacheva	[82]	Sukacheva 1973
2.	Eolepidopterygidae	[?67]	Rasnitsyn 1988
3.	Eolepidopterygidae: *Eolepidopteryx jurassica*	[60]	Rasnitsyn 1983a, Whalley 1986
4.	Eolepidopterygidae: *Daiopteryx rasnitsyni* Skalski	[52]	Skalski 1984b; Whalley 1986
5.	Archaeolepidae: *Archaeolepis mane* Whalley	[69]	Whalley 1985, 1986
6.	Micropterygidae: *Parasabatinca aftimacrai* Whalley	[55]	Whalley 1977, 1986
7.	Micropterygidae: *Palaeosabatinca zherichini* Kozlov	[52]	Kozlov 1988b
8.	?Micropterygidae	[45]	Schlüter 1975, 1978; Whalley 1986
9.	Micropterygidae: *Micropteryx immensipalpa* Kusnezov	[19]	Kusnezov 1941; Kozlov 1988b

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
10.	Micropterygidae	[Miocene]	Kozlov 1988b
11.	Undopterygidae: *Undopteryx sukatshevi* Skalski	[37]	Skalski 1979a; Whalley 1986
12.	Lophocoronidae	[37]	Skalski 1979b; Kozlov 1988b
13.	Hepialidae: *Prohepialus* sp.	[27]	Piton 1940; Kozlov 1988b
14.	Hepialidae	[Priabon]	Harris 1984
15.	Hepialidae: *Prohepialus* sp.	[18]	Jarzembowski 1980
16.	Incurvariidae	[55]	Whalley 1987; Hennig 1981
17.	?Nepticulidae: *Stigmellites*, leaf-mines	[39]	Kozlov 1987, 1988b
18.	Nepticulidae: ?*Nepticula* sp.	[29]	Crane & Jarzembowski 1980; Kozlov 1988b
19.	Incurvariidae: *Adela kuznetzovi* Kozlov	[19]	Kozlov 1987, 1988b
20.	?Gracillariidae: *Bucculatrix platani* (Kozlov)	[39]	Kozlov 1988b
21.	?Noctuidae, egg	[Campan.]	Gall & Tiffney 1983
22.	Tineoidea, caterpillar	[35]	MacKay 1970; Whalley 1986
23.	Heterocera	[18]	Lutz 1987
24.	?Nocutidae: *Palaeochiropterix tupaiodon* Revilliod	[24]	Lutz 1987
25.	Papilionidae: *Praepapilio gracilis* Durden & Rose, Lycaenidae: *Riodinella nympha* Durden & Rose	[23]	Durden & Rose 1978; Kozlov 1988b
26.	Pyralidae: *Glendotricha olgae* Kusnezov, Eucosmidae: *Electresia zalesskii* Kusnezov, Tortricidae: *Tortricidrosis inclusa* Skalski	[19]	Kusnezov 1941; Larsson 1978; Keilbach 1982; Kozlov 1988b
27.	Lycaenidae: *Aquisextana irenai* Théobald	[13]	Théobald 1937
28.	Zygaenidae: *Zygaena miocaenica* Reiss	[2]	Reiss 1936; Naumann 1987

MOUTHPART CLASS 20: SIPHONOMANDIBULATE

Fig. 88

1.	Meloidae larva (subfamily indeterminate)	[19]	Larsson 1978; Keilbach 1982
2.	*Tetraonyx minuscula* Wickham (subfamily indet.)	[15]	Wickham 1914; Wilson 1978a
3.	*Macratia succinea* Abdullah	[19]	Abdullah 1965; Keilbach 1982
4.	*Lithomacratria mirabilis* Wickham	[15]	Wickham 1914; Wilson 1978a
5.	Anthicidae	[6]	Schumann & Wendt 1989
6.	*Praemordella martynovi* Scegoleva-Barovskaya	[60]	Scegoleva-Barovskaya 1929; Crowson 1981
7.	Mordellidae	[53]	Jell & Duncan 1986
8.	Mordellidae	[23]	Wilson 1978a; Grande 1980
9.	*Mordella inclusa* Germar	[19]	Germar 1813; Keilbach 1982
10.	*Tomoxia inundata* Wickham	[15]	Wickham 1914; Wilson 1978a
11.	*Anaspis* sp.	[6]	Schumann & Wendt 1989
12.	Rhipiphoridae	[23]	Wilson 1978a; Grande 1980
13.	*Rhipidius primordalis* Stein	[19]	Stein 1877; Keilbach 1982
14.	Rhipiphoridae	[15]	Wilson 1978a; Grande 1980

MOUTHPART CLASS 21: GLOSSATE
Fig. 91

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
1.	Bethyloid, family indeterminate	[53]	Jell & Duncan 1986
2.	Tiphiidae	[37]	Zherikin & Sukacheva 1973
3.	Pompilidae: *Pompiliopterus ciliatus* Rasnitsyn	[52]	Rasnitsyn 1975
4.	Formicidae	[55]	Hennig 1981
5.	*Angarosphex myrmicopterus* Rasnitsyn	[52]	Rasnitsyn 1975
6.	*Scolia* sp.	[19]	Larsson 1978
7.	*Scolia* sp.	[15]	Handlirsch 1908
8.	Scoliidae	[8]	Rasnitsyn 1980
9.	Masaridae	[52]	Rasnitsyn 1988
10.	Masaridae	[39]	Rasnitsyn 1988
11.	*Curiovespa magna* Rasnitsyn	[39]	Rasnitsyn 1975
12.	*Eumenes projaponica* Piton	[27]	Piton 1940
13.	*Odynerus wilmattae* Cockerell; *Odynerus oligopunctatus* Théobald	[15,13]	Cockerell 1906a; Théobald 1937
14.	*Alastor rottensis* Statz	[8]	Statz 1936
15.	Vespidae	[32]	Wilson 1978a
16.	*Palaeovespa baltica* Cockerell	[19]	Burnham 1978
17.	*Palaeovespa florissanta* Cockerell	[15]	Cockerell 1906a; Théobald 1937
18.	*Vespa nigra* Statz	[8]	Statz 1936
19.	*Baissodes robustus* Rasnitsyn	[52]	Rasnitsyn 1975
20.	*Cretavus sibiricus*	[39]	Sharov 1957a; Rasnitsyn 1975
21.	*Protomutilla dentata* Bischoff	[19]	Bischoff 1915; Keilbach 1982
22.	*Sapyga* sp.	[19]	Larsson 1978
23.	*Archisphex crowsoni* Evans	[57]	Evans 1969
24.	Pemphredoninae	[53]	Jell & Duncan 1986
25.	*Cretosphex incertus* Rasnitsyn	[52]	Rasnitsyn 1975
26.	*Gallosphex cretaceus* Schlüter	[45]	Schlüter 1978
27.	Sphecidae; *Taimyrisphex pristinus* Evans	[39,37]	Evans 1973; Rasnitsyn 1988
28.	*Lisponema singularis* Evans	[35]	Evans 1969
29.	*Crabo succinalis* Cockerell	[19]	Cockerell 1909e; Keilbach 1982
30.	*Passaloecus scudderi* Cockerell	[15]	Cockerell 1906a; Wilson 1978a
31.	Sphecidae	[8]	Bohart & Menke 1976
32.	*Sphex bischoffi* Zeuner	[7]	Zeuner 1931
33.	*Passaloecus munax* Sorg	[6]	Sorg 1986
34.	*Halictus scudderiellus* Cockerell	[15]	Cockerell 1906b; Wilson 1978a
35.	*Osmia antiqua* Heer	[3]	Burnham 1978
36.	*Andrena wrisleyi* Salt	[19]	Salt 1931
37.	*Andrena grandipes* Cockerell	[15]	Cockerell 1906b
38.	*Andrena primaeva* Cockerell	[3]	Burnham 1978
39.	*Melitta willardi* Cockerell	[19]	Burnham 1978
40.	*Anthidium exhumatum* Cockerell	[15]	Burnham 1978
41.	*Megachile amaguensis* Cockerell	[12]	Cockerell 1925a
42.	*Anthidium mortuum* (Meunier)	[8]	Burnham 1978
43.	*Anthophora melfordi* Cockerell; *Tetralonia berlandi* Théobald	[15,13]	Burnham 1978

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
44.	*Xylocopa hydrobiae* Zeuner	[9]	Zeuner 1938
45.	*Xylocopa friesei* Statz	[8]	Burnham 1978
46.	*Anthophorites tonsa* Heer	[3]	Burnham 1978
47.	*Electrapis proava* (Menge)	[19]	Burnham 1978
48.	*Apis henshawi* Cockerell	[8]	Burnham 1978
49.	*Apis armbrusteri* (Armbruster)	[7]	Armbruster 1938; Zeuner 1931
50.	*Apis armbrusteri* (Armbruster)	[2]	Zeuner *et al.* 1976
51.	*Trigona prisca* Michener & Grimaldi	[36]	Michener & Grimaldi 1989a, 1989b
52.	*Trigona eocenica* Kelner-Pillault	[19]	Burnham 1978
53.	*Trigona dominicana* Wille & Chandler	[17]	Wille & Chandler 1964; Burnham 1978
54.	*Trigona silacea* Wille	[11]	Burnham 1978
55.	*Probombus hirsutus* Piton	[27]	Piton 1940; Burnham 1978
56.	*Chalcobombus humilis* Cockerell	[19]	Burnham 1978
57.	*Bombus florissantensis* (Cockerell)	[15]	Cockerell 1906b; Burnham 1978
58.	*Bombus abavus* Heer	[3]	Burnham 1978

MOUTHPART CLASS 22: ENTOGNATHOUS-STYLATE

Fig. 94.

1.	Testajapygidae: *Testajapyx thomasi* Kukalová-Peck	[96]	Kukalová-Peck 1987
2.	Isotomidae: *Rhyniella praecursor* Hirst & Maulik	[104]	Hirst & Maulik 1926; Greenslade & Whalley 1986
3.	Entomobryidae: *Permobrya mirabilis* Riek	[91]	Riek 1976b
4.	Arthropleona	[37]	Zherikin & Sukacheva 1973
5.	Entomobryidae: *Protentomobrya walkeri* Folsom	[35]	Folsom 1937
6.	Isotomidae: *Isotoma protocinera* Handschin, Hypogasturidae: *Hypogastura protoviatica* Handschin	[19]	Larsson 1978; Keilbach 1982
7.	Isotomidae: *Cryptopygus*, Entomobryidae: *Seira*	[17]	Mari Mutt 1983
8.	Entomobryidae: Entomobrya decora ?Nicolet,	[11]	Christiansen 1971; Keilbach 1982
9.	?Neanuridae	[104]	Greenslade 1988
10.	Poduridae: *Podura pulchra* Koch & Berendt	[19]	Koch & Berendt 1854; Keilbach 1982
11.	Smithurinidae: *Smithurinus brevicornis* Koch &	[19]	Koch & Berendt 1854; Keilbach 1982
12.	Smithurinidae: *Sphyrotheca* sp.	[11]	Mari Mutt 1983

MOUTHPART CLASS 23: ECTOGNATHOUS-STYLATE

Fig. 97

1.	*Macrelcama ungeri* (Heer)	[3]	Heer 1849; Zeuner 1939
2.	*Notokistus brodiei* Handlirsch	[69]	Abdullah 1975
3.	Rhysodidae	[17]	Baroni-Urbani *et al.* 1982
4.	Rhysodidae	[Miocene]	Dmitriev & Zherikin 1988
5.	*Avocatinus elongatus* Ponomarenko	[82]	Ponomarenko 1969a
6.	Catiniidae	[52]	Rasnitsyn 1988
7.	*Porrhodromus communis* Tichomirova	[60]	Tichomirova 1968
8.	Leiodidae	[Eocene]	Dmitriev & Zherikin 1988
9.	Leiodidae	[6]	Schumann & Wendt 1989

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
10.	Helodidae	[53]	Jell & Duncan 1986
11.	Eucinetidae	[60]	Rasnitsyn 1988
12.	Eucinetidae	[52]	Rasnitsyn 1988
13.	Eucinetidae	[6]	Schumann & Wendt 1989
14.	*Phymaphoroides antennatus* Motschulsky	[19]	Larsson 1978; Keilbach 1982
15.	Cerylonidae	[37]	Dmitriev & Zherikin 1988
16.	Corylophidae	[Eocene]	Dmitriev & Zherikin 1988
17.	*Corylophus* sp.	[19]	Dmitriev & Zherikin 1988
18.	Corylophidae	[6]	Schumann & Wendt 1989

MOUTHPART CLASS 24: SEGMENTED BEAK

Fig. 100

1.	Lophioneuridae: *Tschekardus hispidus* Vishniakova	[89]	Vishniakova 1981
2.	Permaleurodidae: *Permaleurodes rotundatus* Bekker-Migdisova	[97]	Rohdendorf *et al.* 1961
3.	Protopsyllidae: *Carpenterella curtipennis* Bekker-Migdisova	[60]	Bekker-Migdisova 1968
4.	?Bernaeidae:	[56]	Whalley & Jarzembowski 1985
5.	Bernaeidae: *Bernaea neocomica* Schlee	[55]	Schlee 1970
6.	Psyllidae	[53]	Jell & Duncan 1986
7.	Aleyrodidae: *Aleurodes aculeatus* Menge	[19]	Keilbach 1982
8.	Psyllidae	[18]	Jarzembowski 1976
9.	Psyllidae: Psyllina ("Blattflöhe")	[17]	Schlee & Glockner 1978
10.	Psyllidae	[15]	Wilson 1978a
11.	Psyllidae: Psyllina ("Blattflöhe")	[11]	Schlee & Glockner 1978
12.	Psyllidae	[6]	Barthel & Hetzer 1982
13.	Permaphidopseidae: *Kaltanaphis permiensis* Bekker-	[97]	Rohdendorf *et al.* 1961
14.	?Callaphididae: *Penaphis woollardi* Jarzembowski	[57]	Jarzembowski 1989
15.	Aphidoidea, Coccoidea	[37]	Zherikin & Sukacheva 1973
16.	Canadaphidae: *Canadaphis carpenteri* Essig	[35]	Essig 1937
17.	Pemphigidae	[23]	Wilson 1978a; Grande 1980
18.	Aphididae: *Aphis retrolactens* Menge	[15]	Keilbach 1982
19.	Aphidoidea	[18]	Jarzembowski 1976
20.	Aleyrodina ("Mottenläuse)	[17]	Schlee & Glockner 1978
21.	Aphididae, Coccidae	[15]	Wilson 1978a
22.	Aphidina	[6]	Schumann & Wendt 1989
23.	Archescytinidae: *Permopsylla kuznetskiensis* Bekker-Migdisova	[97]	Rohdendorf 1961
24.	Scytinopteridae: *Scytinoptera* sp.	[86]	Strümpel 1983
25.	Protoposbolidae: *Protoprosbole straeleni* Laurentiaux	[101]	Laurentiaux 1953
26.	Blattoprosbolidae: *Blattoprosbole tomiensis* Bekker-Migdisova	[97]	Rohdendorf *et al.* 1961
27.	Palaeotinidae: *Austroprosboloides vandijki* Riek	[84]	Riek 1973
28.	Prosobolidae: *Permocicada integra* (Bekker-Migdisova	[86]	Rohdendorf 1957

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
29.	Palaeotinidae: *Palaeotinoides shabaravi* Martynov	[73]	Martynov 1937a
30.	?Palaeotinidae: *Apheloscyta mesocampta* Tillyard	[74]	Tillyard 1922, 1923c
31.	Palaeotinidae: *Palaeotinoides haifanggouensis* Hong	[64]	Hong 1983
32.	Palaeotinidae	[57]	Jarzembowski 1984
33.	Palaeotinidae: *Nonnacottella pulcherrima* Whalley &	[56]	Whalley & Jarzembowski 1985
34.	Pereboriidae: *Neuropibrocha ramisubcostalis* Bekker-Migdisova	[97]	Rohdendorf *et al.* 1961
35.	Cixiidae: *Scytocixius* *mendax* Martynov	[87]	Martynov 1937b
36.	Cixiidae: *Mesocisoides fermioneura* Tillyard	[74]	Tillyard 1922
37.	Fulgoridae: *Eofulgoridium kisyl-kiense* Martynov	[73]	Martynov 1937a
38.	Cicadidae: *Liassocicada ignotatus* Brodie	[69]	Whalley 1983
39.	Procercopidae: *Procercopis debilis* Bode	[68]	Bode 1953
40.	Cercopidae: *Hebeicercopis triangulata* Hong	[64]	Hong 1983
41.	Cicadidae: *Cicada proserpina* Weyenbergh	[61]	Kuhn 1961
42.	Cicadellidae	[57]	Jarzembowski 1984
43.	Cicadellidae: *Acocephalites breddini* Meunier	[56]	Whalley & Jarzembowski 1985
44.	Cixiidae: *Mundopoides aptianus* Fennah	[55]	Fennah 1987
45.	Cixiidae	[53]	Jell & Duncan 1986
46.	Fulgoroidea	[37]	Zherikin & Sukacheva 1973
47.	Jascopidae: *Jascopus notabilis* Hamilton	[35]	Keilbach 1982
48.	Fulgoridae, Cercopidae, Cicadellidae	[32]	Mitchell & Wighton 1979
49.	Cixiidae, Fulgoridae, Cercopidae	[23]	Wilson 1978a; Grande 1980
50.	Fulgoridae: *Poeocera nassuta* Germar	[19]	Keilbach 1982
51.	Auchenorrhyncha	[18]	Jarzembowski 1976
52.	Flatidae	[17]	Fennah 1963
53.	Cixiidae, Delphacidae, Fulgoridae	[15]	Wilson 1978a
54.	Cicadellidae	[4]	Palmer 1957
55.	Progonocimicoidea	[?89]	Popov 1980
56.	Progonocimicidae: *Olgamartynova turanica* Bekker Migdisova	[71]	Popov 1982
57.	Progonocimicidae: *Progonocimex jurassicus* Handlirsch	[68]	Popov & Wootton 1977
58.	Progonocimicidae	[57]	Jarzembowski 1984
59.	Progonocimicidae	[46]	Kormilev & Popov 1986
60.	Peloridae	[?Aptian]	Popov 1980
61.	Cuneocoridae: *Cuneocoris geinitzi* Handlirsch	[68]	Handlirsch 1908; Popov & Wootton 1977
62.	Enicocephalidae	[19]	Jarzembowski 1986
63.	Enicocephalidae: *Paenicotechys fossilis* (Cockerell)	[15]	Keilbach 1982a
64.	Dipsocoridae: *Ceratocombus hurdi* Wygodzinsky	[11]	Keilbach 1982
65.	?Hydrocorisae	[76]	Olsen *et al.* 1978
66.	Unnamed family	[69]	Whalley 1985
67.	Veliidae	[53]	Jell & Duncan 1986
68.	Serridae, Veliidae	[32]	Mitchell & Wighton 1979
69.	Hydrometridae: *Eocenometra danica* Anderson	[Eocene]	Anderson 1982
70.	Saldidae, Gerridae, Gelastocoridae	[23]	Wilson 1978a; Grande 1980
71.	Halobatidae: *Halobates* sp.	[19]	Keilbach 1982
72.	Saldidae: *Leptosalda chiapensis* Cobben	[17]	Cobben 1971
73.	Saldidae, Gerridae, Veliidae	[15]	Wilson 1978a

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
74.	Saldidae: *Leptosalda chiapensis* Cobben	[11]	Cobben 1971
75.	Triassocoridae: *Triassocoris myersi* Tillyard	[74]	Tillyard 1923c
76.	Belostomatidae: *Mesonepa* sp.	[69]	Whalley 1985
77.	Corixidae: *Yanliaocorixa chinensis* Lin	[64]	Hong 1983
78.	Belostomatidae: *Mesobelostomum deperditum* Germar	[61]	Kuhn 1961
79.	Naucoridae: *Aidium pleurale* Popov	[60]	Popov 1968
80.	Notonectidae, Naucoridae, Corixidae	[54]	Sanz *et al.* 1988
81.	Gelastocoridae	[53	Jell & Duncan 1986
82.	Gelastocoridae	[23]	Wilson 1978a; Grande 1980
83.	Corixidae: *Corixa* sp.	[19]	Larsson 1978
84.	Notonectidae, Gelastocoridae, Belostomatidae,	[15]	Wilson 1978a
85.	Notonectidae: *Notonecta rotti* Jordan	[8]	Jordan 1953
86.	Pachymeriidae	[69]	Whalley 1985
87.	Pachymeriidae: *Pachymeridium dubium* Geinitz	[68]	Popov & Wootton 1977
88.	Coreidae: *Sinocoris oblonga* Hong	[64]	Hong 1983
89.	Coreidae: *Monstrocoreus quadrimaculatus* Popov	[60]	Popov 1968
90.	Alydidae	[46]	Kormilev & Popov 1986
91.	Pentatomidae	[32]	Mitchell & Wighton 1979
92.	Pentatomidae	[26]	Britton 1960
93.	Pentatomidae	[24]	Lutz 1987
94.	Coreidae	[23]	Wilson 1978a; Grande 1980
95.	Aradidae: *Aradus superstes* Germar	[19]	Keilbach 1982
96.	Lygaeidae, Coreidae, Pyrrhocoridae, Cydnidae	[15]	Wilson 1978a
97.	Lygaeidae: *Procymophyes lithax* Sailer & Carvalho	[4]	Palmer 1957
98.	Archegocimicidae	[69]	Whalley 1985
99.	Sisyrocoridae: *Corynecoris semigranulatus* Bode	[68]	Popov & Wootton 1977
100.	Eocimicidae: *Mesocimex sinensis* Hong	[64]	Hong 1983
101.	Miridae: *Scutellifer karataviensis* Popov	[60]	Popov 1968
102.	Geocorisae	[56]	Whalley & Jarzembowski 1985
103.	Anthocoridae	[53]	Jell & Duncan 1986
104.	Miridae	[46]	Kormilev & Popov 1986
105.	Microphysidae	[37]	Zherikin & Sukacheva 1973
106.	Anthocoridae	[35]	McAlpine & Martin 1969
107.	Cimicidae, Reduviidae	[24]	Lutz 1987
108.	Reduviidae	[23]	Wilson 1978a; Grande 1980
109.	Nabidae: *Nabis lucida* Germar	[19]	Keilbach 1982
110.	Reduviidae: *Empicoris copal* Popov	[17]	Popov 1987
111.	Tingidae, Miridae, Reduviidae	[15]	Wilson 1978a
112.	Miridae: Mirinae	[6]	Barthel & Hetzer 1982
113.	Miridae: *Miomonalonion conoidifrons* Sailer & Carvalho	[4]	Palmer 1957

MOUTHPART CLASS 25: BUCCAL CONE
Fig. 103

Entry No.	**Taxon Corresponding to Entry Number**	**Fossil Insect Locality**	**References**
1.	Lophioneuridae: *Dichentomum tinctum* Tillyard	[90]	Tillyard 1926c; Carpenter 1932a
2.	Mallophaga, family indeterminate	[19]	Keilbach 1982
3.	Hoplopleuridae: *Neohaematopinus relictus* Dubinin	[Pleist]	Laurentiaux 1953

MOUTHPART CLASS 26: MOUTHCONE
Fig. 106

1.	Lophioneuridae: *Dichentomum tinctum* Tillyard	[90]	Tillyard 1926c; Carpenter 1932a
2.	*Tschekardus hispidus* Vishniakova	[89]	Vishniakova 1981
3.	*Zoropsocus tomiensis* BekkerMigdisova	[L. Perm]	Sharov 1973
4.	*Karatavocypha oculata* Vishniakova	[60]	Vishniakova 1981
5.	Lophioneuridae	[57]	Jarzembowski 1984
6.	*Undacypha fumida* Vishniakova	[52]	Vishniakova 1981
7.	*Jantardachus perfectus* Vishniakova	[37]	Vishniakova 1981
8.	*Karatauthrips jurassicus* Sharov	[60]	Sharov 1973
9.	*Nerothrips fritschi* Priesner	[19]	Priesner 1924
10.	Aeolothripidae	[37]	Rasnitsyn 1988
11.	Aeolothripidae	[23]	Wilson 1978a; Grande 1980
12.	*Archankothrips pugionifer* Priesner	[19]	Priesner 1924
13.	*Aeolothrips extinctus* Priesner & Quievreux	[16]	Priesner & Quievreux 1935
14.	Melanothripinae	[4]	Palmer 1957
15.	Seven monofamilial taxa assigned to extinct families, but probably belonging to Heterothripidae	[55]	Zur Strassen 1973; Seeger, in Hennig 1981
16.	?Heterothripidae	[52]	Rasnitsyn 1988
17.	*Protothrips speratus* Priesner	[19]	Priesner 1929
18.	Thripidae ("Ceratothripidae")	[37]	Zherikin & Sukacheva 1973
19.	*Anaphothrips perspicuus* Priesner	[19]	Priesner 1924; Larsson 1978
20.	*Franklinella oligocaenica* Priesner & Quivreux	[16]	Priesner & Quivreux 1935
21.	Phlaeothripidae ("Pygothripidae")	[37]	Zherikin & Sukacheva 1973
22.	*Cephalothrips laticeps* Priesner	[19]	Priesner 1924; Larsson 1978

MOUTHPART CLASS 27: MONOSTYLATE/DISTYLATE
Fig. 109

1.	Bibionidae	[36]	Olsen *et al.* 1978
2.	Xylophagidae	[42]	Dmitriev & Zherikin 1973
3.	Stratiomyiidae	[56]	Whalley & Jarzembowski 1985
4.	*Archocyrtus gibbosus* Ussatchov	[60]	Ussatchov 1968
5.	Acroceridae	[23]	Wilson 1978a; Grande 1980
6.	*Glaesnocodes completinervis* Hennig	[19]	Hennig 1968
7.	*Archinemestrinus karatavicus* Rohdendorf	[60]	Rohdendorf 1968
8.	Tabanidae	[24]	Lutz 1987

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
9.	?Athericidae	[24]	Lutz 1987
10.	*Protobrachyceron liasinum* Handlirsch	[68]	Handlirsch 1908
11.	*Palaeoplatypygus zaitzevi* Kovalev	[65]	Kalugina & Kovalev 1985
12.	*Zarzia* sp.	[37]	Zaitzev 1981
13.	*Proglabellula electrica* Hennig	[19]	Hennig 1967c
14.	*Systropus acourti* Zaitzev	[18]	Zaitzev 1981
15.	*Glabellula kuehnei* Schlüter	[17]	Schlüter 1976
16.	*Megacosmus secundus* Cockerell	[15]	Cockerell 1911
17.	*Praecythera sardii* Théobald	[13]	Théobald 1937
18.	Bombyliidae	[6]	Schumann & Wendt 1989
19.	*Mydas* sp.	[15]	Cockerell 1913b
20.	Asilidae	[23]	Wilson 1978a; Grande 1980
21.	*Asilus angustifrons* Loew	[19]	Loew 1850; Hennig 1967c
22.	*Senoprosopis antiquus* James	[15]	James 1939
23.	*Protoloewinella keilbachi* Schumann	[6]	Schumann 1984
24.	*Thereva pinguis* (Loew)	[19]	Loew 1850; Keilbach 1982
25.	Scenopinidae	[42]	Dmitriev & Zherikin 1988
26.	*Protempis antennata* Ussatchov	[60]	Ussatchov 1968
27.	Empididae	[57]	Jarzembowski 1984
28.	*Trichinites cretaceus* Hennig	[55]	Hennig 1970
29.	*Ecommocydromia difficilis* Schlüter	[45]	Schlüter 1978
30.	*Empis orapaensis* Waters	[43]	Waters 1989a
31.	Empididae	[40]	Langenheim *et al.* 1960
32.	*Cretoplatypalpus archaeus*	[37]	Kovalev 1978
33.	Empididae	[35]	McAlpine & Martin 1969
34.	Empididae	[32]	Wilson 1978a
35.	Empididae	[23]	Wilson 1978a; Grande 1980
36.	*Empis externa* (Loew)	[19]	Loew 1850; Larsson 1978
37.	*Empis infossa* Melander; *Trachydromia theobaldi* Timon-David	[15,14]	Melander 1949; Timon-David 1943
38.	Empididae	[6]	Schumann & Wendt 1989
39.	*Retinitus nervosus* Negrobov	[37]	Negrobov 1978
40.	Platypezidae	[55]	Kovalev 1985
41.	Ironomyiidae	[52]	Rasnitsyn 1988
42.	Sciadoceridae	[55]	Kovalev 1985
43.	*Metopina goeleti* Grimaldi	[36]	Grimaldi 1989
44.	Syrphidae	[37]	Kovalev 1985
45.	Conopidae	[55]	Hennig 1971a

MOUTHPART CLASS 28: DISTYLATE/TETRASTYLATE

Fig. 112

1.	Chaoboridae: *Praechaoborus tugnuicus* Kalugina	[66]	Kalugina & Kovalev 1985
2.	Bibionidae	[76]	Olsen et *al.* 1978
3.	*Protolbiogaster rhaetica* Rohdendorf	[73]	Rohdendorf 1974
4.	Anisopididae	[60]	Rasnitsyn 1988
5.	Anisopodidae	[35]	McAlpine & Martin 1969

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
6.	Anisopodidae	[23]	Wilson 1978a
7.	*Rhyphus splendidus* Meunier	[19]	Meunier 1904c; Keilbach 1982
8.	Anisopodidae	[15]	Wilson 1978a
9.	Anisopodidae	[6]	Schumann & Wendt 1989
10.	Xylophagidae	[42]	Dmitriev & Zherikin 1988
11.	Stratiomyiidae	[56]	Whalley & Jarzembowski 1985
12.	*Archocyrtus gibbosus* Ussatchov	[60]	Ussatchov 1968
13.	*Archinemestrinus karatavicus* Rohdendorf	[60]	Rohdendorf 1968b
14.	Tabanidae	[24]	Lutz 1987
15.	?Athericidae	[24]	Lutz 1987
16.	*Palaeobrachyceron handlirschi* Kovalev	[66]	Kovalev 1981
17.	*Kubekovia accessoria* Kovalev	[65]	Kalugina & Kovalev 1985
18.	*Palaeoptiolina scobloi* Kovalev	[62]	Kovalev 1982
19.	*Rhagioempis antennata* Rohdendorf	[60]	Rohdendorf 1938; Kovalev 1982
20.	Aff. *Ptiolina* sp.	[57]	Jarzembowski 1984
21.	*Atherimorpha festuca* Jell & Duncan	[53]	Jell & Duncan 1986
22.	Rhagionidae	[52]	Rasnitsyn 1988
23.	Rhagionidae	[37]	Zherikin & Sukacheva 1973
24.	*Protovermileo electricus* Hennig	[19]	Hennig 1967a
25.	*Symphotomyia subtrita* Cockerell; *Rhagio primaevus* Théobald	[15,13]	Cockerell 1911; Théobald 1937
26.	Rhagionidae	[6]	Schumann & Wendt 1989
27.	*Palaeoplatypygus zaitzevi* Kovalev	[65]	Kalugina & Kovalev 1985
28.	*Mydas* sp.	[19]	Cockerell 1913b
29.	Asilidae	[23]	Wilson 1978a; Grande 1980
30.	*Thereva pinguis* (Loew)	[19]	Loew 1850; Keilbach 1982
31.	*Psilocephala hypogaea* Cockerell	[15]	Cockerell 1909b; Irwin & Lyneborg 1987
32.	Scenopinidae	[42]	Dmitriev & Zherikin 1973
33.	*Protempis antennata* Ussatchov	[60]	Ussatchov 1968
34.	*Retinitus nervosus* Negrobov	[37]	Negrobov 1978
35.	Platypezidae	[55]	Kovalev 1985
36.	Ironomyiidae	[52]	Rasnitsyn 1988
37.	Ironomyiidae	[42]	Rasnitsyn 1988
38.	*Cretonomyia pristina* McAlpine	[35]	McAlpine 1973
39.	Sciadoceridae	[55]	Kovalev 1985
40.	*Metopina goeleti* Grimaldi	[36]	Grimaldi 1989
41.	Syrphidae	[37]	Kovalev 1985
42.	Conopoidea: Conopidae	[55]	Hennig 1971a

MOUTHPART CLASS 29: HEXASTYLATE

Fig. 115

1.	Tipulidae	[78]	Olsen *et al.* 1978
2.	Blepharoceridae	[42]	Dmitriev & Zherikin 1988
3.	?*Paltostomopsis ciliatus* Cockerell	[18]	Cockerell 1916b
4.	*Praemacrochile stackelbergi* Kalugina	[66]	Kalugina & Kovalev 1985
5.	*Eolimnobia geinitzi* Handlirsch	[68]	Handlirsch 1908; Rohdendorf 1974

Entry No.	*Taxon Corresponding to Entry Number*	*Fossil Insect Locality*	*References*
6.	*Mesopsychoda dasyptera* Brauer, Redtenbacher & Ganglbauer	[67]	Brauer *et al.* 1887
7.	*Eopericoma zherichini* Kalugina	[62]	Kalugina & Kovalev 1985
8.	*Tanyderophryne multinervis* Rohdendorf	[60]	Rohdendorf 1962, 1974
9.	*Phlebotomites brevifilis* Hennig	[55]	Hennig 1972b
10.	*Syncorax* sp.	[35]	Quate & Vockeroth 1981
11.	*Nemopalpus molophinus* Edwards	[19]	Schlüter 1978
12.	Psychodidae	[18]	Jarzembowski 1976
13.	*Nemopalpus hennigianus* SchluPh"ter 1978	[17]	Schlüter 1978
14.	*Trichomyia antiquaria* Quate	[11]	Quate 1961
15.	Psychodidae	[6]	Schumann & Wendt 1989
16.	Thaumaleidae	[E. Cret]	Rasnitsyn 1988
17.	Simuliidae	[60]	Rasnitsyn 1988
18.	Simuliidae	[53]	Jell & Duncan 1986
19.	*Simulium importunum* Meunier	[19]	Meunier 1904a; Keilbach 1982
20.	Simuliidae	[10]	Cuffey *et al.* 1982
21.	Simuliidae	[6]	Schumann & Wendt 1989
22.	*Simulidium priscum* Westwood	[36]	Grogan & Szadziewski 1988
23.	?*Forcipomyia* sp.	[45]	Schlüter 1978
24.	*Culicoides kaluginae* Remm	[37]	Remm 1986
25.	?*Culicoides casei* Grogan & Szadziewski	[36]	Grogan & Szadziewski 1988
26.	*Lasiohelea creta* Boesel	[35]	Boesel 1937
27.	*Ceratopogon flagellus* Meunier	[19]	Meunier 1904c; Keilbach 1982
28.	Ceratopogonidae	[17]	Schlee & Glockner 1978
29.	Ceratopogonidae	[10]	Cuffey *et al.* 1982
30.	*Culicoides obscuratus* Statz	[8]	Statz 1944c
31.	*Atrichopogon* sp.	[6]	Schumann & Wendt 1989
32.	*Dasyhelea australis* Palmer	[4]	Palmer 1957
33.	*Architendipes tschernovskii* Rohdendorf	[62]	Rohdendorf 1974
34.	Chironomidae	[66]	Kalugina 1983
35.	?*Podonomus rotundatus* Kalugina	[65]	Kalugina & Kovalev 1985
36.	*Oryctochlus vulcanus* Kalugina	[62]	Kalugina & Kovalev 1985
37.	?*Protendipes* sp.	[60]	Kalugina & Kovalev 1985
38.	*Libanoclites neocomicus* Brundin	[55]	Brundin 1976
39.	Tanypodinae	[54]	Jell & Duncan 1986
40.	*Cretodiamesa taimyrica* Kalugina	[37]	Kalugina 1976
41.	?*Tvetenia* sp.	[36]	Grimaldi *et al.* 1989
42.	*Smittia veta* Boesel	[35]	Boesel 1937
43.	Chironomidae	[24]	Lutz 1987
44.	Chironomidae	[23]	Wilson 1978a; Grande 1980
45.	*Chironomus obscurus* Meunier	[19]	Meunier 1899a; Larsson 1978
46.	Chironomidae	[17]	Schlee &: Glockner 1978
47.	*Chironomus pristinus* Melander; Chironomidae	[15,13]	Théobald 1937; Melander 1949
48.	Chironomidae	[10]	Cuffey *et al.* 1982
49.	*Pelopia thienemanni* Statz	[8]	Statz 1944c
50.	Chironomidae	[6]	Schumann & Wendt 1989
51.	*Calopsectra* sp.	[4]	Palmer 1957
52.	*Praechaoborus tugnuicus* Kalugina	[66]	Kalugina & Kovalev 1985

MOUTHPART CLASS 30: TRISTYLATE
Fig.118

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
1.	Protomeropeidae: *Altajopanorpa brevis* Martynova	[97]	Rohdendorf *et al.* 1961
2.	*Tarwinia australis* Jell & Duncan	[53]	Riek 1970a; Jell & Duncan 1986
3.	Pulicidae	[53]	Riek 1970a; Jell & Duncan 1986
4.	Leporid host biogeography	[Paleogene]	Traub & Rothschild 1983
5.	Marsupial host biogeography & fossil record	[L. Cret]	Traub & Rothschild 1983
6.	*Palaeopsylla klebsiana* Dampf	[19]	Larsson 1978; Keilbach 1982
7.	Cricetid host biogeography	[Paleogene]	Traub & Rothschild 1983
8.	Chiropteran host biogeography & fossil record	[Paleogene]	Jepsen 1966; Traub & Rothschild 1983
9.	*Saurophthirus longipes* Ponomarenko	[52]	Ponomarenko 1976

MOUTHPART CLASS 31: TUBULOSTYLATE
Fig. 121

1.	Conopidae	[55]	Hennig 1971a
2.	*Eophlebomyia claripennis* Cockerell	[23]	Cockerell 1925b
3.	*Glossina armatipes* Cockerell	[15]	Cockerell 1907b, 1909c, 1917b
4.	*Ornithomya rottensis* Statz	[8]	Maa 1966
5.	Earliest bat fossil for streblid parasites: *Icaronycteris index* Jepsen	[23]	Jepsen 1966; Grande 1980
6.	Earliest bat fossil for nycteribiid parasites: *Icaronycteris index* Jepsen	[23]	Jepsen 1966; Grande 1980

MOUTHPART CLASS 32: SIPHONOSTYLATE
Fig. 124

1.	*Noctuites* sp.	[Campan.]	Gall & Tiffney 1983
2.	*Noctuites haidingeri* Heer	[5]	Heer 1849; Kozlov 1988b
3.	*Noctuites gersdorfi* Kernbach	[Pliocen]	Kernbach 1967

MOUTHPART CLASS 33: REDUCED TROPHIC
Fig. 127

1.	Protopsyllididae: *Triassaphis cubitus* Evans	[79]	Evans 1956
2.	*Mesococcus asiaticus* Bekker-Migdisova	[73]	Bekker-Migdisova 1959
3.	*Eomatsucoccus sukachevae* Koteja	[52]	Koteja 1988c
4.	Margarodidae	[37]	Koteja 1986a
5.	*Electrococcus canadensis* Beardsley	[35]	Beardsley 1969
6.	*Acreagris crenata* Koch & Berendt	[19]	Koch & Berendt 1854; Ferris 1941

(REDUCED TROPHIC, continued)

Entry No.	Taxon Corresponding to Entry Number	Fossil Insect Locality	References
7.	*Monophlebus simplex* Scudder	[15]	Scudder 1890; Koteja 1986a
8.	*Matsuococcus saxonicus* Koteja	[6]	Koteja 1986b
9.	Ortheziidae	[37]	Koteja 1988c
10.	*Ochyrocoris electrina* Menge	[19]	Menge 1856; Koteja 1986a
11.	Pseudococcidae	[37]	Koteja 1986a
12.	Pseudococcidae	[19]	Spahr 1988
13.	Pseudococcidae	[11]	Koteja 1986a
14.	*Sucinikermes kulickae* Koteja	[19]	Koteja 1988b
15.	Eriococcidae	[37]	Koteja 1986a
16.	*Kuenowicoccus pietrzeniukae* Koteja	[19]	Koteja 1988a
17.	Eriococcidae	[11]	Koteja 1986a
18.	Coccidae	[37]	Koteja 1986a
19.	Coccidae	[35]	Spahr 1988
20.	*Coccus termitinus* Menge	[19]	Menge 1856; Keilbach 1982
21.	Coccidae	[17]	Spahr 1988
22.	Diaspididae	[37]	Koteja 1986a
23.	Diaspididae	[19]	Spahr 1988
24.	Diaspididae	[11]	Koteja 1986a
25.	Diaspididae: ("coccide")	[9]	Zeuner 1938; Koteja 1986a
26.	*Praemordella martyknovi* Segoleva-Barovskaya	[60]	Segoleva-Barovskaya 1929; Crowson 1981
27.	Mordellidae	[53]	Jell & Duncan 1986
28.	*Mordella priscula* Cockerell	[23]	Cockerell 1925c
29.	*Mordella inclusa* Germar	[19]	Germar 1913; Keilbach 1982
30.	*Tomoxia inundata* Wickham	[15]	Wickham 1914
31.	*Anaspis* sp., *Mordellistena* sp.	[6]	Schumann & Wendt 1989
32.	*Rhipidius primordalis* Stein	[19]	Stein 1877; Keilbach 1982
33.	*Myodites burmiticus* Cockerell	[Pleist.]	Cockerell 1917a; Keilbach 1982
34.	Cupedidae: *Eocupes lukjanovitschi* Rohdendorf	[97]	Rohdendorf et al. 1961; Ponomarenko 1969
35.	*Mengea tertiaria* Menge	[19]	Menge 1866; Larsson 1978
36.	*Protelencholax schleei* Kinzelbach 1979	[17]	Kinzelbach 1979
37.	*Stichotrema eocaenicum* (Haupt)	[22]	Haupt 1950; Kinzelbach & Lutz 1985
38.	*Myrmecolax glaesi* Kinzelbach	[17]	Kinzelbach 1983
39.	Cosssidae: *Gurnetia durranti* Cockerell	[18]	Cockerell 1921; Kozlov 1988b
40.	Cossidae: *Adelopsyche frustans* Cockerell	[23]	Cockerell 1926
41.	Zygaenidae: *Zygaena miocaenica* Reiss	[2]	Reiss 1936; Naumann 1987
42.	Xyelidae: *Triassoxyela foveolata* Rasnitsyn	[82]	Rasnitsyn 1964
43.	Ichneumonidae: *Tanychorella parvula* Rasnitsyn, Megalyridae: *Cleistogaster buriatica* Rasnitsyn	[66]	Rasnitsyn 1975
44.	Megaspilidae: *Allocotidus bruesi* Muesebeck	[40]	Muesebeck 1963
45.	Maimetshidae: *Maimetsha arctica* Rasnitsyn, Stigmaphronidae: *Stigmaphron orphne* Rasnitsyn	[37]	Rasnitsyn 1975
46.	?Lygoceridae: ?*Lygocerus dubiatus* Brues	[35]	Brues 1937
47.	Ceraphronidae: *Conostigmus succinalis* Brues	[19]	Brues 1940b; Köningsmann 1978a
48.	Heloridae: *Protohelorus mesozoicus* Kozlov	[60]	Kozlov 1968
49.	Pelecinidae: *Iscopinus baissicus* Kozlov	[39]	Kozlov 1974; Köningsmann 1978a
50.	Trupochalcidae: *Trupochalcis inops* Kozlov, ?Vanhorniidae, Serphitidae	[37]	Zherikin & Sukacheva 1973; Kozlov 1975; Rasnitsyn 1975